SOURCES OF INDIVIDUAL VARIABILITY IN SENSITIVITY TO THE ENVIRONMENT

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SOURCES OF INDIVIDUAL VARIABILITY IN SENSITIVITY TO THE ENVIRONMENT

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Sensitivity to environmental context has been of interest for many years, but the nature of individual differences in environmental sensitivity has become of particular focus over the past 2 decades. What is particularly uncertain are the neural variables and processes that mediate the effects of environment on developmental outcomes. Accordingly, in this dissertation, a neurobehavioral model of sensitivity to the environment is proposed and tested in a large sample of human subjects. First, the different patterns of environmental sensitivity are defined to identify the significant factors involved in the manifestation of these patterns. Second, the mechanisms of neurobiological reactivity underlying variation in sensitivity to the environment are proposed by providing an organizing threshold model of elicitation of emotional neurobiology by environmental context. Third, developmental predictions of the model are explored, namely that reactivity of emotional systems will reflect endogenous sensitivities and environmental history. Finally, an empirical investigation of this model is presented. The sensitivity of three emotional systems (social bonding, incentive approach, and stress reactivity) was assessed by exposing participants ($N = 398$) to stimuli that elicit their activity. In particular, 1) *soft touch* is a potent social reward activating the social bonding system; 2) *anticipation of winning a monetary reward* activates the incentive motivation system; and 3) *uncertainty of an aversive noise* activates the stress response. First, the magnitude of soft touch, monetary reward and uncertainty was varied (i.e., number of brush strokes, amount of monetary reward, and degree of uncertainty), and participants reported immediate emotional feelings in response to

each intensity level. Second, participants engaged in an associative conditioning procedure in which each stimulus was paired with a neutral context. The degree of conditioning represents how deeply the emotional experiences were processed to affect learning, and hence, plasticity. Results show that momentary responses to each emotional stimulus strongly predicted degree of associative conditioning and that emotional sensitivities were related in expected ways to early environmental experience and personality traits. These findings suggest that the proposed emotional systems are mechanisms of adaptation to the environment, and that the function of these systems reflect environmental history.

BIOGRAPHICAL SKETCH

Sarah Moore received her B.S. in psychology at the University of Maryland, where she researched both child attachment and evolutionary genetics. Her interests in the interaction between early social environment and genetic sensitivities led to her work at Cornell University. At Cornell, Sarah studied the neurobiological basis of traits and learned a variety of quantitative strategies. She applied this knowledge to developmental questions on the biological factors influencing how individuals encounter and respond to social environments. These experiences led to the development of her theoretical model of individual differences in sensitivity to the environment that laid the foundation for her doctoral research.

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Introduction

The Relationship Between Humans and Environment

How organisms respond to and adapt to their environments over the course of development is a critical topic bridging biology, psychology, and neuroscience. Biological functioning, and consequences for behavior and well-being are intrinsically linked to environmental signals: from the activity of neurons to broader-scale networks, biological machinery is guided by signals from the environment that regulate the expression of genes and strengthen neural connections. These ongoing interactions between biology and environment shape the organism, molding its characteristics to contextual surroundings.

In human development, understanding the impact of particular experiences on developmental processes is desirable from both a basic science and translational standpoint. Human experiences, such as poverty, trauma, education, and social support, are developmentally linked to who leads happy and successful lives, and who suffers from mental dysfunction and unhealthy behaviors. Uncovering how social environments become biologically embedded informs how individual differences develop, as well as strategies for intervening with corrective experience.

In this dissertation, I explore the neurobiological underpinnings of this relationship between person and environment. The focus is on the biological characteristics of individuals that shape 'sensitivity', or specifically, what aspects of the environment are responded to and internalized in a lasting manner. I first propose a framework for understanding the neurobiological processes that account for sensitivity to environmental experiences. This framework is then explored in an investigation of neurobiological sensitivity, in which the sensitivity of biological systems is assessed in the laboratory, and related to environmental history and current behavioral tendencies.

Background on Theories of Environmental Sensitivity

For nearly a century, there has been growing interest in the manner in which the environment affects physiological and psychological functioning. The World Wars clearly illustrated the devastating psychiatric effects of aversive conditions on soldiers, as has every other war, natural disaster, and trauma since. Using animal models, Selye (1970) pioneered physiological research on what came to be known generally as *stress* (Selye, 1970), while concurrently Hinkle (1974) initiated work on the effects of everyday life contexts on human psychiatric and medical disorders. Importantly, it became clear that there is significant individual variation in response to stressors. This fact led to conceptual advances concerning how genetic vulnerabilities, or diatheses, might be aggravated by life stress, resulting in the emergence of any number of psychiatric disorders (Depue, 1979; Gottesman & Shields, 1972; Mendel, 1973; Monroe & Simons, 1991).

More recently, there has been an extension of these earlier diathesis-stress concepts to the manner in which individuals generally differ in their response to environmental contexts of *both* adverse and enriching qualities. In this growing research area, characteristics of individuals have been identified that appear to be markers of sensitivity to the environment, whether the environment is adverse or beneficial. These characteristics include polymorphisms of various genes that affect the functioning of dopamine (DA) or serotonin (5-HT), indices of physiological reactivity, and temperamental traits. Here, I consider the broad patterns and concepts of these findings.

Initially, three groups of researchers brought attention to a major pattern of response to the environment, which they refer to by different terms as *Biological Sensitivity to Context* (BSC; Ellis & Boyce, 2008; Ellis, Essex, & Boyce, 2005; Ellis, Jackson, & Boyce, 2006; Ellis, Boyce, Belsky, Bakermans-Kranenburg, & van Ijzendoorn, 2011), *Differential Susceptibility* (DS; Belsky et al., 2009; Belsky, Bakermans-Kranenburg, & van IJzendoorn, 2007; Belsky & Pluess, 2009), and *Sensory Processing Sensitivity* (SPS; Aron & Aron, 1997; Aron, Aron, & Jagiellowicz, 2012). Though they tend to emphasize somewhat different aspects, the common theme in these concepts is that individuals vary in their response to environmental contexts of *both* positive and adverse valence, and therefore manifest variation in socio-emotional and cognitive developmental outcomes to those contexts. This response pattern is conceived not in terms of vulnerability or risk, as in the diathesis-stress model, but rather as reflecting normal trait variation in the sensitivity of the central and/or autonomic nervous systems to stimulation of any valence, due either to variation in the stress response system (BSC) and/or in genetic polymorphisms associated with neurotransmitter function (DS). Based on empirical findings, there is also some degree of concordance that variation in negative emotionality may be a temperamental trait associated with the development of sensitivity to environmental stimulation, though as noted by Belsky and Pluess (2009) negative emotionality may have received disproportionate emphasis due to the preponderance of studies concerned with negative developmental outcomes.

The BSC-DS-SPS environmental response pattern is displayed in Figure 1, where the x-axis defines type and magnitude of environmental context, ranging from adverse to positive, to which individuals are exposed; and the y-axis displays the type and magnitude of socio-emotional and cognitive developmental outcome, also ranging from negative to positive. With respect to BSC-DS-SPS, the level of environmental reactivity is represented in the figure by the simple slopes of the outcome regressed on the environmental predictor for two extremes in environmental reactivity: high and low sensitivity, which together create the cross-over interaction used to identify the BSC-DS-SPS pattern.

Figure 1.

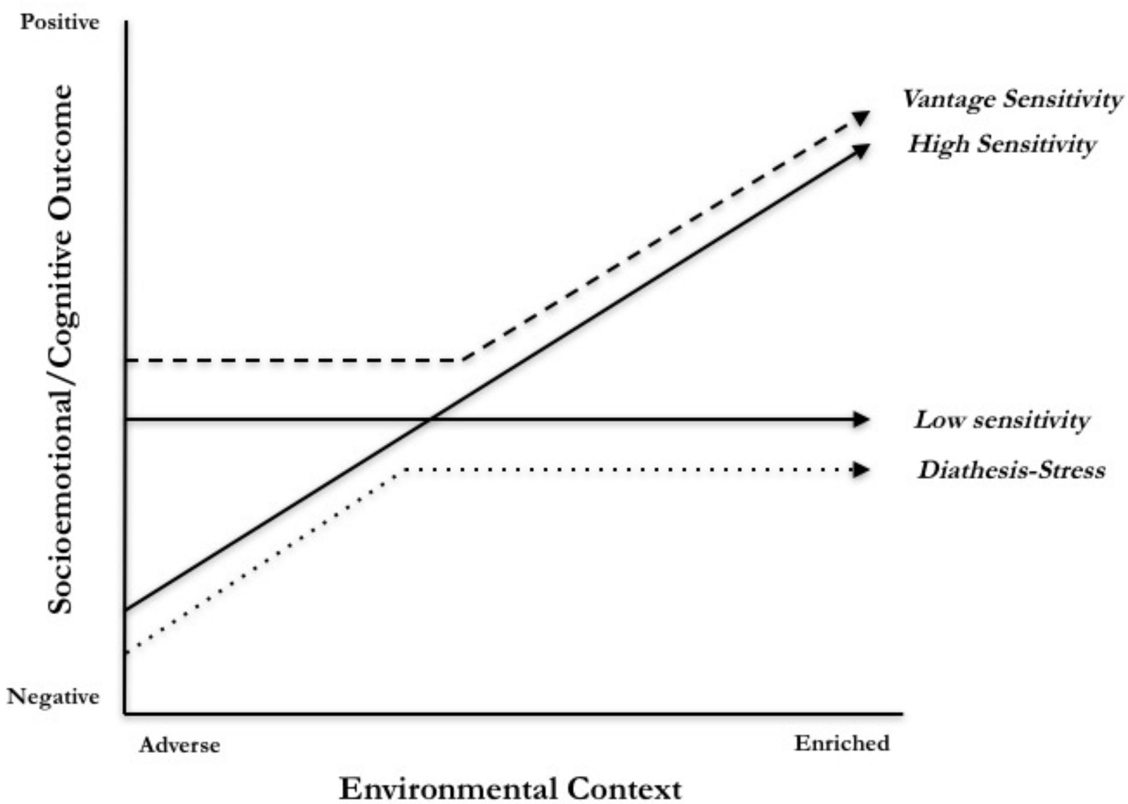


Figure 1 also illustrates the characteristics of two additional patterns of environmental sensitivity in the research literature. One pattern is *Vantage Sensitivity* (VS; Pluess & Belsky, 2013; Sweitzer et al., 2012). A VS pattern is manifested when individuals vary particularly in their response to positive environmental contexts, some showing a pattern of enhanced benefit from exposure to positive circumstances and a simultaneous resilience (as opposed to mere insensitivity) to negative circumstances. In addition to similar genetic variables that relate to the BSC-DS-SPS pattern, a number of studies have found that high trait levels of positive emotionality, which may moderate the effects of rearing experiences on positive developmental outcomes (Belsky & Pluess, 2009; Pluess & Belsky, 2013), may also characterize many VS individuals. Such individuals may be particularly reactive to environmental contexts that are characterized as highly rewarding in that positive emotionality is a natural affective response to reward (Depue & Collins, 1999; Depue & Fu, 2013; Depue & Morrone-Strupinsky, 2005; Pluess & Belsky, 2013).

A final reactivity pattern shown in Figure 1 is diathesis-stress, which reflects an inherent neurobiological vulnerability that is activated by stress. As pointed out by Belsky and Pluess (Belsky & Pluess, 2009), the predominance of diathesis-stress interpretations may be due to the fact that research has been strongly biased towards psychopathology and indicators of environmental risk, considering that a predisposition to maladaptive outcomes such as depression in the face of adversity does not make evolutionary sense. However, the stress-sensitive phenotypes associated with psychopathology may well be adaptive, with their manifestation corresponding with a behavioral profile that enhances survival in the face of uncertainty and danger (Beery & Francis, 2011; Meaney, 2010).

Figure 1 does not imply any etiologic commonality of underlying sensitivity or susceptibility factors across reactivity patterns; however, there is good reason to suspect that common causal variables account for these patterns. First, it is the case that many of the genetic polymorphisms and temperamental traits are similarly identified as markers for multiple patterns (Bakermans-Kranenburg & van Ijzendoorn, 2011; Ellis et al., 2011; Pluess & Belsky, 2013). Genetic polymorphisms affecting DA function, and negative emotionality, for instance, are both markers of BSC-DS-SPS and VS. Second, many of these markers capture common neurobiological function, although at different levels of analysis (e.g., physiological stress reactivity and negative emotionality). Third, the environmental factors to which individuals vary in responsiveness in this literature share common features. An analysis of the empirical work cited in comprehensive reviews and meta-analyses of the environmental sensitivity literature (Bakermans-Kranenburg & van Ijzendoorn, 2011; Belsky & Pluess, 2009; van Ijzendoorn, Belsky, & Bakermans-Kranenburg, 2012; van Ijzendoorn & Bakermans-Kranenburg, 2015) is shown in Appendix A.

In this analysis, the environmental contexts from this collection of empirical studies are characterized into broad categories on the basis of emotional-motivational features. The content of the reviewed environmental measures is most relevant to three emotional-motivational systems and reflect ubiquitous human social experience, including: (i) incentive reward (e.g., all forms of rewarding contexts, parenting, programs that improve literary and working memory skills important for achievement goals, SES reflecting level of opportunities and incentives for achievement); (ii) social reward and attachment (e.g., maternal sensitivity and nurturance, expressed emotion, communication, attachment security, positive interventions, social connections, institutionalized care); and (iii) uncertainty and stress (e.g., childhood maltreatment and deprivation, negative parenting, prenatal stress, early family adversity and conflict, brief and extended stressors, low SES). Note that many commonly applied environmental measures likely capture relative levels of all three of these stimulus classes. For instance, sensitive parenting captures both levels of rewarding social interaction and stress over inconsistency, neglect or harsh care. Taken together, the environmental contexts that are measured in the sensitivity literature are largely overlapping in terms of their emotional-motivational content.

What is missing from the existing literature is a clear conceptualization of what emotional neurobiological processes really account for variation in sensitivity to human social environments. The specific biological pathways linking markers of environmental sensitivity and particular environments to outcomes have yet to be addressed. How do these various emotionality markers fit together to create dimensions of sensitivity? What really underlies variation in vulnerability to stressful environments, susceptibility to any kind of experience, and vantage sensitivity?

In the remainder of this chapter, I address the neglected neurobiological underpinnings of sensitivity. First, I propose a comprehensive neurobiological model of sensitivity to the environment. I identify the neural variables that define a dimension of environmental sensitivity reflecting the relative strengths of positive and negative emotionality. Second, I discuss the implications of this neurobiological model. Third, I propose how to target variation in environmental sensitivity experimentally as an empirical test of this theoretical model.

Conceptualizing the Nature of Sensitivity to the Environment

From a neurobiology perspective, the concept of sensitivity incorporates two components which interact to define the threshold at which individuals respond to the environment: (i) characteristic or trait magnitude of neural reactivity, and (ii) magnitude of eliciting stimuli. That is, sensitivity defines the functional relationship between reactivity of neurobiological systems and environmental stimulation, and it is the interaction of these that determines outcome. Variation in neural reactivity to the environment can be profitably conceptualized within a threshold model of reactivity, because it defines (i) the interactive relationship between neural functioning and environmental stimulation, and (ii) the effects of this interaction on attention to and encoding of environmental contexts. The relation between these two variables is represented in Figure 2 as a trade-off function (White 1986), where the magnitudes of pairs of values (of stimulation and neural reactivity) specify a diagonal representing the minimum threshold value for response facilitation. This minimum threshold value represents the construct of *sensitivity*. Because the two input variables are interactive, independent variation in either one not only modifies the probability of response facilitation, but it also simultaneously modifies the value of the other variable that is required to reach a minimum threshold for facilitation.

Figure 2.

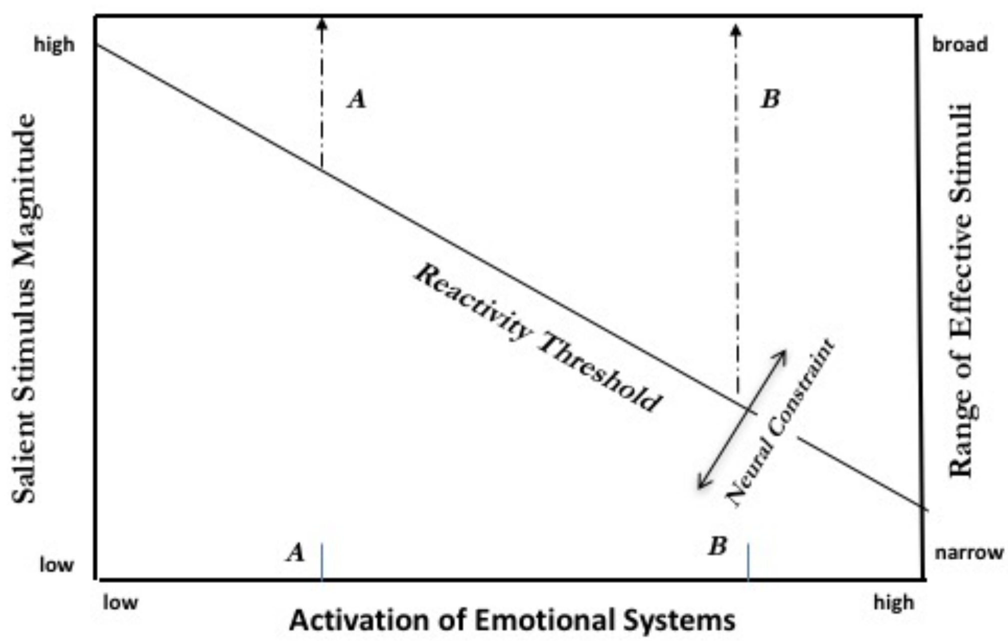


Figure 2 distinguishes between two contributors to the minimum threshold and consequently, sensitivity. The first consists of emotional-motivational systems (horizontal axis in Figure 2) that are activated by specific, broad classes of stimulus (left vertical axis), and which thereby influence the reactivity threshold (diagonal in Figure 2) to specific eliciting cues. Critical variables consist of (i) DA value-encoding neurons that facilitate incentive motivation and positive emotionality in contexts of reward; (ii) beta-endorphin neurons that activate endogenous opiates (OP) and oxytocin (OT), which both facilitate social bonding and attachment processes in affiliative contexts; and (iii) central coticotropin releasing hormone (CRH) neurons that facilitate anxiety and negative emotionality in contexts of uncertainty and potential danger.

While there are certainly other emotional systems that likely contribute to environmental reactivity, the selected emotional-motivational systems respond to broad classes of eliciting stimulus that are part of the environmental contexts, both positive and negative, present in life (consistent with the measured environments in the environmental sensitivity literature, discussed above and in Appendix A). Hence, these emotional-motivational systems are subject to frequent activation, providing the means of adapting to those contexts. Importantly, trait variation in the functioning of an emotional neural system, e.g., due to polymorphisms in genes that significantly affect neurotransmitter functioning, will result in variation along the horizontal dimension of Figure 2 and, hence, in variation in *sensitivity* to corresponding eliciting emotional stimuli in the environment.

The second major neural contributor to sensitivity is not elicited by specific classes of stimulus and is not associated with the facilitation of specific emotional-motivational systems. Each of these neuromodulators provides an inhibitory, or 'constraining' modulation of the threshold of various neural circuit functions, the influence of which is illustrated in Figure 2 as a bidirectional line located perpendicular to the threshold diagonal. Increasing values of constraint would increase the threshold value required for behavioral facilitation (i.e., an increase or decrease in constraint would raise or lower the entire threshold line vertically). Therefore, variables with general effects across emotional systems, such as 5-HT and norepinephrine (NE), are unified under the construct of *neural constraint*, which has a range of effects from *lability* to *rigidity* of circuit functioning (low and high constraint, respectively). It is worth noting that the generalized effects of these transmitters would be expected to affect stimulus reactivity in general, regardless of valence, and therefore are concordant with the general neural sensitivity concepts discussed by previous researchers (Aron et al., 2012; Belsky & Pluess, 2009; Boyce & Ellis, 2005; Ellis et al., 2011).

Combined, the strength of emotional-motivational systems and neural constraint shape the extent that environments have enduring effects on plasticity. This point can be better made with an example following Figure 2, where two individuals with divergent trait levels are demarcated: *A* (low trait level) and *B* (high trait level). For this example, I will consider the incentive-motivation system, such that individual B, due to a combination of reactive DA-incentive motivation circuitries and lower constraint, has greater emotional responsiveness to incentive rewards relative to individual A. First, as displayed on the left vertical axis of Figure 2, the salient stimulus magnitude required to elicit a response increases with increasing threshold value, such that the magnitude required to elicit a response falls *beneath* the threshold line. Individual *A* requires a salient stimulus of higher magnitude relative to individual B to surpass his or her reactivity threshold for the elicitation of a neural response. Individual *B*, then, is responsive to weaker incentive stimuli relative to individual *A*.

Second, trait differences in incentive activation, then, have marked influence on the *range* of effective (i.e., reward- and behavior-inducing) incentive stimuli. This is illustrated in the right vertical axis, where the range of effective stimuli for eliciting a response can be viewed as those falling *above* the reactivity threshold line. Increasing trait levels of DA activation (x-axis) are associated with an increasing efficacy of weaker effective stimuli and, thus, with an increasing range of effective incentive stimuli. In Figure 2 individuals *A* and *B* have a narrow versus broad range, respectively, represented by their respective dashed vertical lines. The broader range for individual *B* suggests that, on average, *B* will experience more *frequent* elicitation of positive emotional experiences associated with reward.

Third, if individual *B* experiences more frequent and more enhanced reward to incentive stimuli, then variation in DA reactivity by incentive stimuli may not only influence the level of experienced reward, but also lead to variation in (i) attentional capture by, and prioritizing for neural processing of, incentive sensory cues; and (ii) the strength of DA-facilitated associative processes that link neutral stimuli with reward (Phillips, Ahn, & Howland, 2003; Wassum, Ostlund, Balleine, & Maidment, 2011). The outcome of higher emotional responsiveness to incentives would thus be a stronger and more elaborate encoded memory network of positive incentives and associated context in individual B. Such differences in the encoding of memory representations of salient contexts could have marked effects on future incentive-motivated behavior through the operation of cognitive processes of working memory integrated in prefrontal brain regions. In prefrontal regions, symbolic central representations of the salient context associated with reward can be held on-line as a means of a) "reliving" and predicting the expected reward from engagement with a salient context, and b) guiding motivated approach to a goal (Rolls, 1999; Waterhouse, Gould, & Bekavac, 1996). Thus, individuals *A* and *B* in Figure 2 may develop differences in their capacity to facilitate over time subjective reward and incentive-motivated behavior due to differentially encoded central representations of salient contexts and their expected outcome *(*Depue & Collins, 1999; Depue & Fu, 2013*)*.

This discussion suggests that variation in sensitivity (response threshold) to environmental context will result across development in variation in the strength and breadth of processing and encoding the environment. This is concordant with the emphasis of researchers in the environmental sensitivity literature on the plasticity effects of variation in sensitivity, where increased neural sensitivity results in experience being registered more easily and deeply (Aron et al., 2012; Belsky & Pluess, 2009). Such effects would be accompanied by strengthening and maintenance of emotional and constraint neural systems themselves via activity-dependent long-term potentiation processes. Thus, neural reactivity to stimuli can translate across development into variation in enduring behavioral tendencies.

Below, I describe the two major components of sensitivity to the environment, and their relationships to enduring behavioral tendencies, or personality traits, in more detail. This discussion includes the specific neurobiological variables whose functioning contributes to variation in emotional reactivity and neural constraint.

Specific Emotional-Motivational Systems

The horizontal axis in Figure 2 represents variation in specific emotional systems that are elicited by specific classes of stimulus and that facilitate specific emotional-motivational patterns. Emotional-motivational systems can be conceived of as behavioral patterns that evolved to increase adaptation to classes of stimuli critical to survival. Three emotional-motivational systems that apply very broadly to important human experience, as demonstrated in the analysis in Appendix A, are incorporated in the current model of sensitivity.

First, the mammalian incentive system evolved to motivate approach to the critical stimulus class of rewards (Depue & Collins, 1999; Gray, 1973; McNaughton & Gray, 2000). Extensive work in humans and animals has linked DA function to the incentive approach system.

Specifically, DA projections from the ventral tegmental area (VTA) to the nucleus accumbens encode the incentive value of environmental cues. DA projections to cortical areas facilitate the formation of contextual ensembles as memory networks of valuable stimuli and their associated contexts. These connections enhance future approach behavior towards environments encoded as beneficial. Variability in this incentive system has direct implications for motivated, approach behavior: higher DA reactivity would be associated with (i) broader contextual networks of cues associated with incentive reward, (ii) more frequent reactivation of DA by these contextual cues, and thereby (iii) maintenance of incentive-motivated behavior towards reward goals.

Second, the social bonding system, which activates behavioral responses to social affiliation cues, evolved to promote attachment between mates, caregivers and offspring, and individuals comprising small in-groups (Depue & Morrone-Strupinsky, 2005; Dunbar, 2010; Machin & Dunbar, 2011). Variation in two neuropeptides: OP and OT, is relevant to reactivity of the bonding system to social cues. Endogenous endorphins are released to social attachment cues, especially soft touch, which leads to positive affective states and associative conditioning of neutral contexts to reward. OT is also responsive to social circumstances, enhancing the downstream effects of social engagement on reduced stress and the formation of social memories. Thus, variation in OP and OT may be significant contributors to the threshold to respond in social contexts, and to the degree that social cues in the environment are processed in depth. Variation in this emotional system would thus affect the extent that social interactions, and social cues in the environment lead to the formation of affiliative memories and pleasant feelings surrounding social figures, and ultimately the promotion and maintenance of social bonding behavior.

Third, the stress-response system describes the activation of anxiety and negative affect to environmental conditions that denote potential harm (e.g., the dark in humans) in order to promote attention to the environment and a cognitive search for resolution of the uncertainty (Davis & Whalen, 2001; Depue & Fu, 2011; Rapee & Barlow, 2002; Tellegen & Waller, 2008). A central network of CRH neuron populations provide integrated responses to environmental stressors, inducing a state of prolonged anxiety accompanied by aversive contextual conditioning. CRH facilitation of arousal and consolidation of emotional cues and contexts could act to facilitate attention, memory, and subsequent engagement with contexts that are positive in nature as well. For instance, both rewards and stress enhance facilitatory effects of CRH on VTA DA neurons, influencing plasticity of DA responses for future responding to that context (Saal, Dong, Bonci, & Malenka, 2003; Wanat, Hopf, Stuber, Phillips, & Bonci, 2008). Thus, CRH activity enhances reactivity to stressful as well as non-stressful salient cues in the environment, with its effects on anxiety and upregulation of stress reactivity depending on the presence or absence of environmental adversity.

In temperament and personality, it is proposed that variation in neural sensitivity to the above critical stimulus classes underlies higher-order traits, though a seamless conformation between emotional system and personality trait is not likely. From this perspective, Extraversion/positive emotionality may reflect the activity of the incentive motivation system (Depue & Collins, 1999), Social Closeness or Agreeableness activity of the social bonding system (Depue & Morrone-Strupinsky, 2005), and Neuroticism/negative emotionality, in part, activity of an anxiety system (Depue & Fu, 2012; McNaughton & Gray, 2000). Thus, the current model explains why markers of emotionality at many levels of analysis, including genes encoding neurotransmitters, physiological reactivity, and temperament and personality, relate to responsiveness to environmental factors. Specifically, findings that temperamental traits serve as markers of sensitivity might reflect the role of underlying emotional systems promoting plasticity processes and behavioral adaptation to the environment.

Neural Constraint

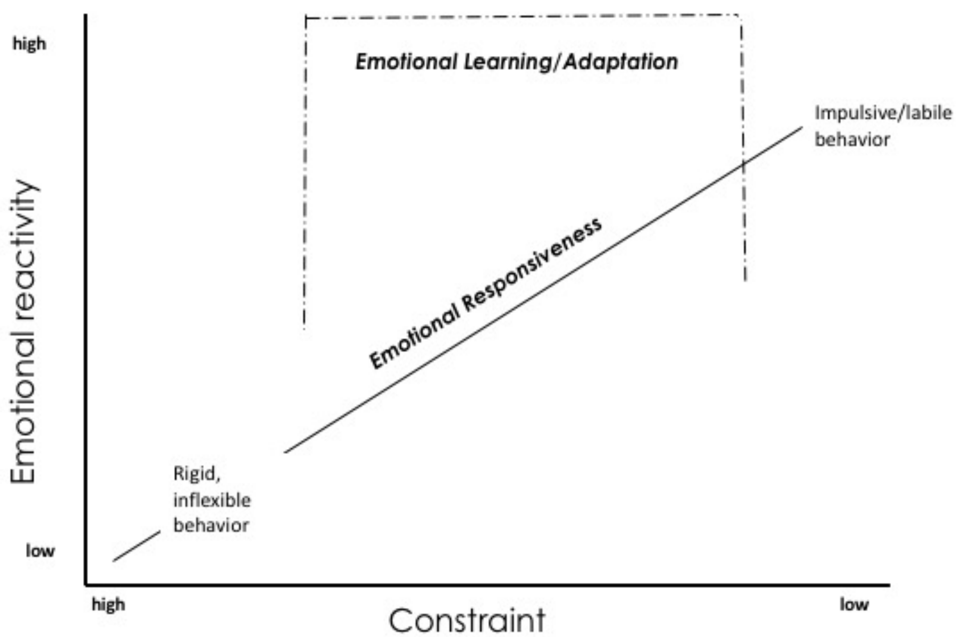
In contrast to variables related to specific emotional responses, there exist a number of neural variables that do not appear to be associated with any specific emotional-motivational behavioral system, and rather exert non-specific inhibitory effects over neural circuits, affecting the threshold of reactivity of neural systems, regardless of the valence of stimuli. Variation in these neural variables, referred to as neural constraint, would result in variation in the magnitude of constraint or inhibitory influence over reactivity in emotional neural circuitries subserving motivated behavior, represented by the bidirectional line located perpendicular to the threshold diagonal in Figure 2 above. Here, I focus on the functions of two particular variables as they relate to neural constraint: 5-HT and NE.

5-HT serves as a general modulator of neural activity and behavior in response to environmental inputs. Empirical literature indicates that 5-HT is a key modulator of the flow of neural signals representing incoming sensory information (Depue & Spoont, 1986; Spoont, 1992), and that 5-HT is related to the capacity of regulatory circuitries to inhibit emotional processes in response to salient, emotionally-laden stimuli in particular (Cools, Roberts, & Robbins, 2008). In general, then, 5-HT functioning can be conceptualized as a critical variable in modulating a general threshold for neural and behavioral responding. This is supported by its broad distribution and involvement in a diverse array of psychological processes, from motor and sensory processes to cognition, attention, emotion, and affiliation.

NE neurons in the locus coeruleus (LC) are activated by salient environmental stimuli of any valence, and have widespread projections with three major downstream effects. First, NE serves to reduce the threshold of sensory neurons that process *relevant* cues, while raising the threshold for neurons processing irrelevant cues, thereby increasing the discrimination between relevant and irrelevant environmental information (Aston-Jones & Cohen, 2005). Second, in combination with stress-reactivity circuitries, NE activity modulates arousal states that aid the formation and retrieval of emotional memories, contributing to the extent that contexts are registered deeply in emotional memory (Berridge & Waterhouse, 2003). Third, LC NE activity plays a *dynamic* role, enhancing the shift between the ventral fronto-parietal attention system that detects changes in salient information, and the dorsal fronto-parietal attention pathways that maintain the efficient operation of task-responding to current, relevant stimuli (Bouret & Sara, 2005).

Together, these functions of 5-HT and NE form a dimension of neural constraint, or overarching control of the processing of salient features from the environment. At very high levels of constraint, there is a very high threshold for the detection of salient emotional cues in the environment, the output of emotional circuitries for higher level processing of emotional cues, and for the facilitation of emotional behavior. At very low levels of constraint and a very low threshold, emotional cues in the environment lead to easy elicitation of neural processing, accompanied by hypervigilance and the flooding of neural systems. Extreme levels of constraint would thus be maladaptive: very high constraint would be related to rigidity and inflexibility in adapting to the emotional environment, and very high constraint would relate to hyperarousal and emotional dysregulation. Thus, the optimal level of constraint for attending to cues of potential importance and adaptive responding would be somewhere in the midrange. As displayed in Figure 3, moderate constraint over emotional responsiveness enhances efficacy in incorporating salient emotional cues into sensory, perceptual, attentional and cognitive processes, and hence learning about those environments.

Figure 3.



In personality, a fourth higher-order trait of Behavioral Constraint or Conscientiousness (reflecting a dimension of impulsivity; Tellegen & Waller, 2008) may reflect the concept of Neural Constraint (Carver et al., 2008; Carver & Miller, 2006; Depue & Fu, 2012). Behavioral constraint is an overarching personality dimension of impulsivity that reflects variation in inhibitory modulation of emotional, motor, cognitive and sensory responses (Carver & Miller, 2006; Carver et al., 2008; Depue, 1995; Depue & Collins, 1999; Depue & Fu, 2011; Depue &

Spoont, 1986; Spoont, 1992; Tellegen & Waller, 2008; Zald & Depue, 2001). Thus, behavioral constraint may reflect the behavioral expression of neural constraint proposed in Figure 2 above.

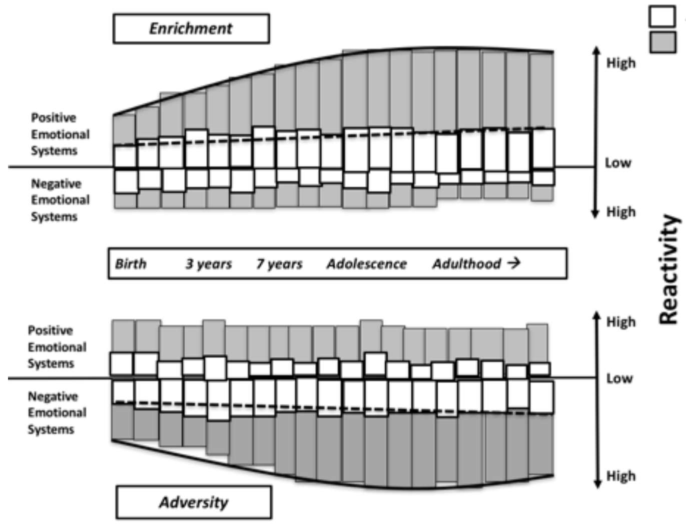
Just as emotional circuitries are modified and elaborated with exposure to eliciting emotional stimuli, the regulatory circuitries of neural constraint are similarly expected to be modified by experience. For instance, when environments are supportive and stimulating, regulatory capacity over stress and the direction of behavior towards incentive goals and social interactions is exercised and strengthened. In the face of uncontrollable stressors, cognitive resources are directed to potential threats to survival, leading to more hypervigilance and negative arousal in response to stressors, and less ‘practice’ at directing resources towards planful, regulated behavior to achieve incentive and social goals.

Implications of Model

Thus far, in outlining the contributions of the neural systems that account for emotional-motivation processing and neural constraint to environmental sensitivity, I have focused on the role of each of these systems in processing salient cues in the environment in depth, leading to plasticity and emotional learning. An important implication of this model is that neural systems themselves are subject to plasticity based on the frequency and magnitude of their elicitation–i.e., their functional properties are activity-dependent, and thereby are subject to long-term potentiation processes that are activated by environmental stimulation.

This suggests that (i) the neurobiological reactivity underlying environmental sensitivity is dependent on the frequency and magnitude of environmental input across time, and (ii) the relative strength of the various emotional-motivational systems will depend on the predominant nature of environmental contexts present during development. In other words, the predominant nature of environmental contexts across development, in interaction with endogenous functioning of these neural systems, will result in differential weighting and persistent strengthening of the neural threshold for eliciting differentially the major emotional-motivational systems and their associated processes (incentive reward motivation, social bonding, and anxiety). The end result of these processes may well be the emergence of differential developmental trajectories in neural, emotional, and environmental sensitivity patterns. For instance, Figure 4 illustrates differential developmental trajectories in two individuals of high (B) versus low (A) emotional-motivational reactivity in predominant contexts of adversity and enrichment. As shown by the bars throughout each developmental stage, these two individuals show different magnitudes of effects of environmental adversity or enrichment on the development of their emotional systems, where both contexts have stronger effects on individual B's emotional development relative to individual A. Thus, individual B, due to more intense and frequent responding to environmental context and greater internalizing of these experiences in neural networks, demonstrates increasingly greater effects of *both* adversity and enrichment across development relative to individual A. Stabilization of environmentally-induced plasticity in the neurobiological systems underlying positive and negative emotionality may produce additive effects of experience over time, leading to diverging trajectories of individual B versus A in the magnitude of positive or negative emotional reactivity across development as a function of predominant environmental conditions.

Figure 4.



Due to these developmental processes, patterns of environmental reactivity may well demonstrate specificity to particular social contexts (Belsky et al., 2007; Belsky & Pluess, 2009; Caspi & Moffitt, 2006), as particular types of cues and contexts surrounding predominant experiences are encoded into memory networks. Thus, specific types of contexts may become increasingly capable of eliciting their respective emotional-motivational systems in the future. Consider parenting sensitivity as the predominant environmental factor, a variable that is frequently assessed in the environmental sensitivity literature. Parenting sensitivity assessments capture behaviors that engage the social bonding system (warm and comforting embraces in response to distress, expressed affection), the incentive system (smooth and coordinated interactions and supportive encouragement that facilitates infant exploration and goal acquisition), and the stress response system (intrusive behavior that inhibits play, signs of depression, apathy towards infant, unease with the infant's distress and inability to calm and soothe; McElwain & Booth-Laforce, 2006).

Sensitive parenting would favor the activation of the social bonding and incentive motivation systems by cues associated with contexts of warm affection/secure attachments, and encouragement towards productive goals, respectively. When infants become distressed, the ability of sensitive parents to soothe and regulate the infant enhances the encoding of stressors as controllable and attachment figures as dependable resources. Through repeated instances of stress and resolution, skills of self-regulation and problem solving are developed. The end result would be (i) enhanced synaptic connections within the child's incentive approach and social bonding circuitries, (ii) easier elicitation of these systems by positive social experiences, (iii) down-regulation of anxiety and stress reactivity, and iv) strengthening of regulatory capacity via 5-HT and NE modulated attentional and memory networks.

In contrast, insensitive parenting provides an adverse environment that more frequently activates the child's anxiety system, rendering parenting itself as a source of uncontrolled stress for the infant. In these cases, the child's social bonding system is more frequently activated by withdrawal or loss of social rewards, and the incentive system becomes biased towards infrequent, immediate rewards rather than longer-term rewarding goals that require parent facilitation and guidance. Memory networks would encode attachment figures as unreliable or rejecting, social resources as scarce, and the contextual surroundings as unpredictable and aversive. Anxiety and stress reactivity might then be up-regulated, creating hypervigilance and deficits in emotion regulation, potentially to the extent of inhibiting the child's incentive approach system – a devastating outcome for child achievement.

In these ways, the relative strength of positive and negative emotionality would reflect the interaction between the child's endogenous emotional sensitivities at birth and the predominant environmental context provided by parents. Both of these influences contribute to which of the child's emotional systems is activated most frequently, and thus which is relatively strengthened over time. Moreover, in supportive and safe environments, optimal regulatory capacity over emotional responses provided by neural constraint is expected, versus dysregulation in contexts of heightened stress. Thus, the interplay of the neurobiological components of environmental sensitivity with predominant environmental contexts leads to differential trajectories of emotional behavior patterns and developmental outcomes.

An Empirical Investigation of the Proposed Model

Taken together, there are three novel insights into sensitivity to the environment raised by the proposed model that warrant further study. First, sensitivity is a multivariate construct, but to date has only been simplistically identified using single markers (a genetic polymorphism, a gauge of physiological reactivity or single temperamental trait). The first aim of this dissertation is thus to identify variation in environmental sensitivity comprehensively by experimentally quantifying the sensitivity of critical emotional systems. Second, the model predicts that the development of environmental sensitivity, including specific emotional sensitivities and constraint, is molded by predominant environmental contexts across development. The second aim of this work is to test whether previous environmental factors do indeed relate in expected ways to current emotional sensitivities and constraint. Third, the proposed model suggests that higher-order behavioral traits reflect the contribution of emotional sensitivities and environmental factors across developmental history. The third aim is to test whether emotional sensitivity assessed in the laboratory and early environmental factors predict broader personality dimensions.

Aim 1: Quantify Environmental Sensitivity Experimentally. The proposed model suggests that to capture variation in sensitivity to the environment, that both the sensitivity of individual emotional systems, and the tendency to process emotional cues in depth and internalize the experience should be considered. This means that emotional responsiveness should be assessed in two ways. First, the intensity of each class of emotional cue will be varied to capture the magnitude of an emotional stimulus required to elicit neural and behavioral responses (i.e., a response threshold). Second, participants will be exposed to repeated, mild presentations of emotional cues in combination with pictures of neutral faces. Faces represent a socially relevant context to which an emotional experience can become *associatively conditioned*. That is, with repeated associations of a neutral face with the presented emotional cues, the emotional content of the situation becomes learned, and the face itself elicits an emotional response in the absence of the unconditioned, primary stimulus. The degree of associative conditioning to each emotional cue represents the degree that the experience was processed in depth. In other words, conditioning is a gauge of emotional learning capacity for the emotional system at hand. It is hypothesized that momentary reactivity to each emotional stimulus will influence the degree of contextual conditioning, consistent with the notion that a lower threshold for responding to emotional cues enhances the breadth of contextual conditioning or learning about the surrounding environment.

Finally, combining scores across emotional systems will provide an index of momentary reactivity and propensity to condition across emotional systems. According to the model, neural constraint is a common, overarching inhibitory influence upon emotional processing. Thus, if neural constraint does provide equivalent inhibitory modulation for each system, these gauges of momentary reactivity and conditioning propensity are predicted to capture variation in constraint upon emotional reactivity and depth of processing.

Aim 2: Environmental Predictors. According to the proposed model, the predominant nature of environmental contexts across development will result in differential strengthening of emotional systems, such that supportive, enriched environments would enhance the activation and strengthening of social bonding and incentive systems, and stressful environments would strengthen stress reactivity. Thus, to address the second aim, prior environmental experiences, including multiple aspects of the home environment (e.g., parenting quality, conflict, resources), will be assessed as predictors of experimental indices of positive and negative emotional reactivity and learning. It is hypothesized that enriching and supportive environments will promote responsiveness of the incentive reward and social bonding systems, whereas stressful or adverse environments will predict upregulated stress reactivity, both in terms of momentary reactivity and emotional learning.

Aim 3: Biology, Environment, and Personality Outcomes

According to the proposed model, underlying neurobiological reactivity of emotional systems accounts for findings indicating that particular temperamental and personality traits are markers of sensitivity to the environment. The model also predicts that both neurobiological factors and predominant environmental contexts mold trajectories of broader behavioral patterns captured by personality. This third aim is addressed by comprehensive assessment of personality dimensions, and by modeling the effects of experimental gauges of sensitivity and early environments on these traits. It is hypothesized that sensitivity of reward systems will relate to sociality and approach-related traits, and that sensitivity of the stress system will relate to anxiety. It is also hypothesized that gauges of general sensitivity, using a combination score of threshold and emotional learning across systems, will relate to behavioral constraint.

Method

Overview

To quantify environmental sensitivity, participants are characterized in the laboratory in terms of both momentary response thresholds and propensity to condition to incentive reward, social reward, and stress. To assess early experiences and personality traits, participants also complete retrospective measures on family conflict and relationships with parents and comprehensive personality measures via an online survey.

Participants

Participants comprised $N = 398$ young adults (age range 18-31 years; 91% 18-21 years; 67% female) recruited at Cornell University who elected to participate for research credit. The sample self-identified as 46% European American, 26% Asian/Asian American, 12% Hispanic, 7% African American, 4% Middle Eastern or East Indian and 5% 'other'. The study was reviewed and approved by the Institutional Review Board; all participants provided informed consent. Participants completed the online survey prior to visiting the laboratory for emotional sensitivity experiments. Some students completed the online survey, but failed to show up for their laboratory appointment ($n = 41$). For these cases, survey data was used for the calculation of principle components, as larger sample sizes enhance the identification of stable solutions (see below).

Experimental Procedures

To assess sensitivity to emotional stimuli, psychological responsiveness to aversive cues, incentive rewards, and social rewards is assessed. Tasks were selected that have already demonstrated the ability to elicit robust emotional responses in terms of behavior and the neural circuitries of interest in the experimental literature. These manipulations include the presentation of an aversive tone at uncertain times to induce stress (Herry et al., 2007); a reaction time button-press task in which the participant wins a monetary reward if he or she is 'fast enough', which elicits incentive reward-related dopamine activity (Knutson, Westdorp, Kaiser, & Hommer, 2000); and soft brushing of the forearm by a trained experimenter to activate the release of endogenous endorphins in the brain and social reward-related feelings of warmth and pleasantness (McGlone, Wessberg, & Olausson, 2014). Moreover, well established associative conditioning procedures were applied (see below) for assessment of emotional learning.

Momentary Emotional Reactivity/Threshold. To assess momentary emotional reactivity or response threshold, participants were exposed to varying levels of intensity of incentive rewards, social reward, and stress, and then immediately rated their emotional responses. Reward tasks were presented prior to the uncertainty task to ensure feelings of anxiety did not color responses to the rewards. Overviews of each of the three threshold tasks are displayed in Figures 5-7.

First, in the social reward condition, participants' forearms were brushed by an experimenter (who is out of the subject's view), varying the brush strokes from 1 to 3. Brush strokes occurred one after the other for 4'' each. Following each trial, the participant rated on his or her monitor the level of warmth and pleasantness experienced from the brushing. To avoid habituation to the brush strokes, intervals are 30'', and the first round of each intensity level (randomized) occurred before the incentive reward task, and the second round occurred after. Thus, there were two repetitions per intensity level. This task quantifies the threshold for responding to a powerful social reward (soft touch) for the promotion and maintenance of human bonds.

Second, participants rated excitement, enthusiasm, and elation after playing for 1, 2, 3, or 4 tickets towards a $100 lottery in a timed button press task. The subject was instructed to push the button upon the onset of a smiley face in a variable position on the computer monitor, and that the response time must be faster for increasing numbers of tickets ‘on the line’, such that it is the most difficult to win 4-ticket trials, and easiest to win 1-ticket trials. Trials consisted of 4’’ of anticipation, accompanied by text indicating the number of tickets to be played for in the current trial, followed by a rating of excitement, followed by the the presentation of the smiley face, which remained on the screen until the response was made. Participants then received feedback on whether or not they were ‘fast enough’ for 2’’, and a running total of their tickets was updated. By rating excitement associated with the pursuit (button pressing) for the reward prior to feedback, this task captured threshold for responding to reward specifically associated with incentive motivation. Each intensity level was repeated 2 times and trial order was randomized.

Third, participants were exposed to trials in which they anticipated an aversive popping noise to assess threshold for responsiveness to uncertainty. A trial consists of 4’’ of anticipation, accompanied by a probability on the screen of receiving the tone (0, 25, 50, 75 and 100 % probability), followed by a rating of how tense, nervous or anxious they feel, followed by tone administration of the popping noise or no noise (in accordance with probabilities). The participant then again rated feelings of anxiety after the tone, so that negative feelings in anticipation of the tone (which reflects stress to uncertainty) could be dissociated from negative feelings associated with the sound itself. Each intensity level was repeated 2 times and trial order was randomized.

Figure 5.

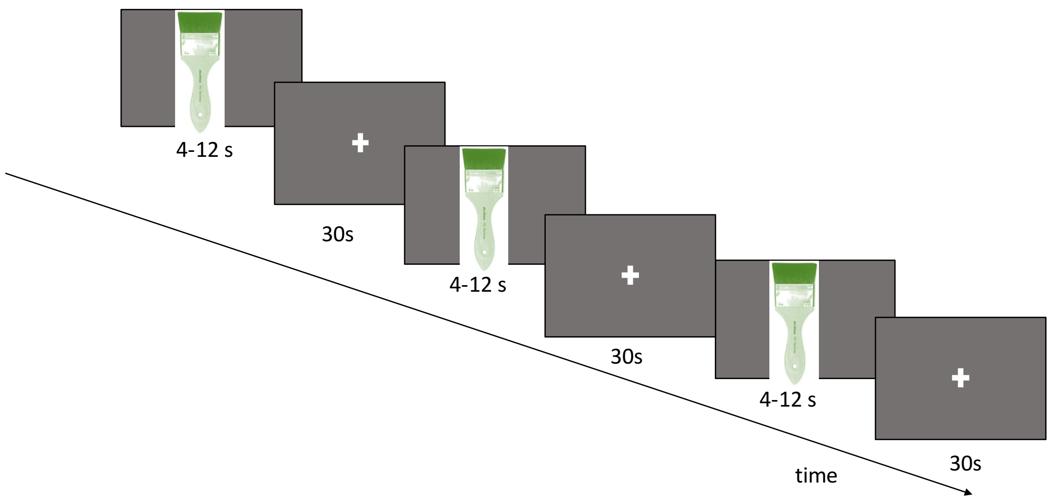


Figure 6.

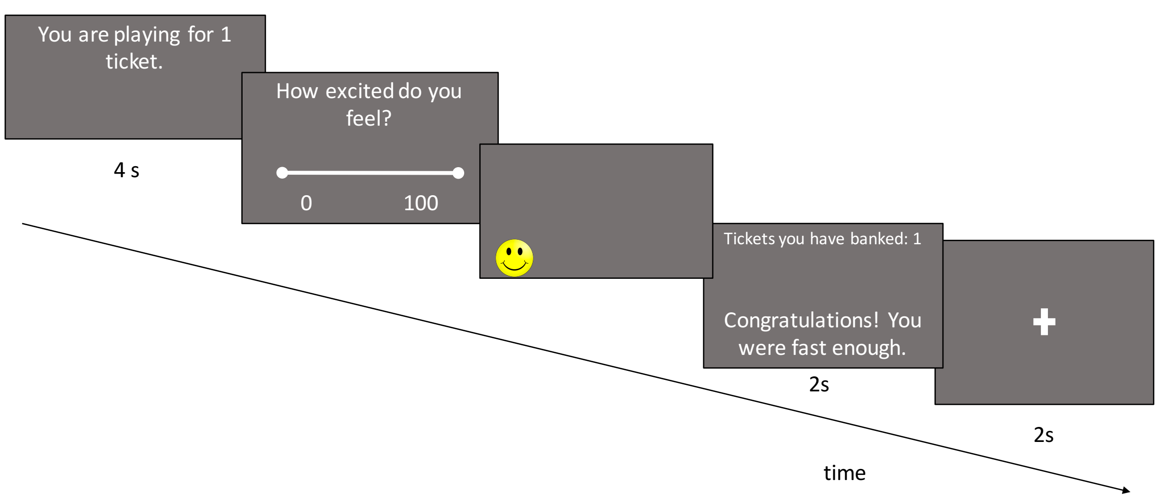
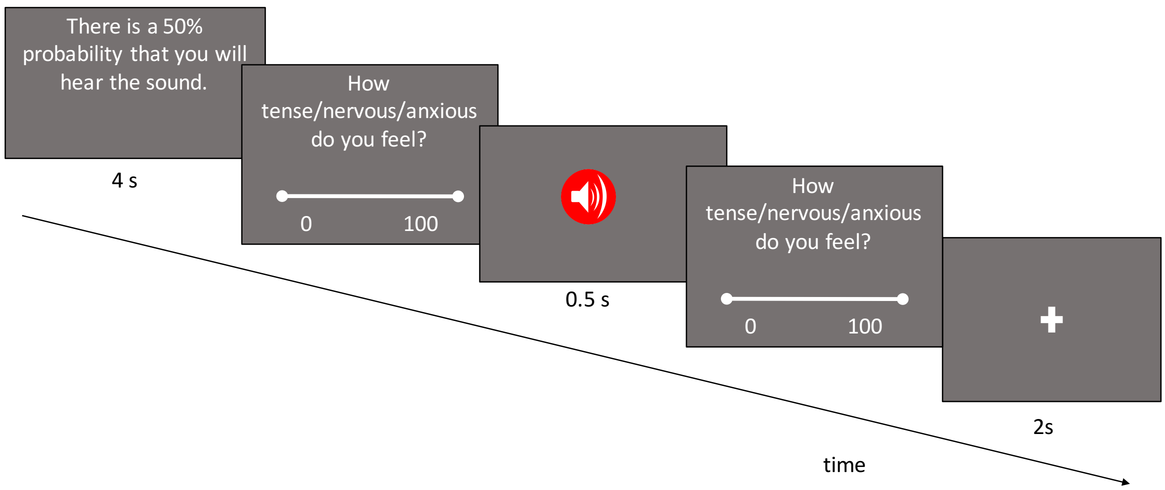
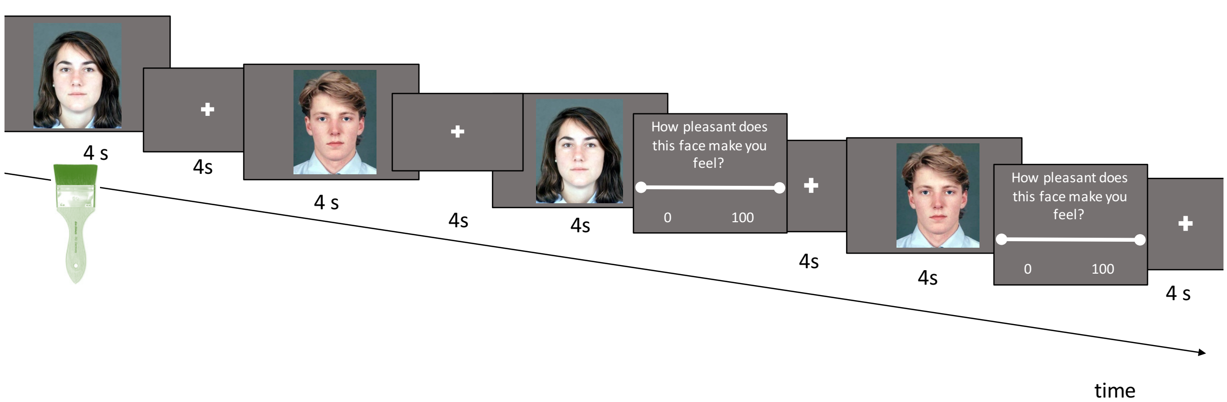


Figure 7.



Emotional Learning/Reflection. In conditioning procedures, participants were exposed to repeated, mild presentations of emotional cues in combination with pictures of neutral faces. Faces represent a socially relevant context to which an emotional experience can become associatively conditioned. That is, with repeated associations of a neutral face with the presented emotional cues, the face itself becomes associated with affective value and capable of eliciting an emotional response in the absence of the unconditioned, primary stimulus. In this task, each condition was again separate and presented in the order indicated above (social reward, incentive, reward, and uncertainty). Each emotional stimulus condition included 2 neutral faces that were either paired (CS+; the face stimulus became conditioned to the emotional experience) or not paired (CS-; the face remained neutral) with the emotional stimulus. The CS+ was conditioned with a 50% partial reinforcement schedule, and thus the participant received the popping sound, a monetary reward (1 ticket), or one brush stroke to the forearm 50% of the time that the CS+ was presented. Face ratings were obtained using the same scales as the above threshold tasks on every unpaired (no tone, no monetary reward, or no brushing) presentation of the CS+ to ensure that psychological responses to the CS+ were not contaminated by the unconditioned stimulus (popping sound, monetary reward, or brushing). Face ratings of the CS- were also made on ½ of the face presentations so that the ratings of the CS+ across time reflect divergence from neutral ratings. The four trial types (CS+ paired, CS+ rated, CS-, CS- rated) were randomized and presented for 10 cycles, for a total of 40 trials per condition. Faces were presented for 4''. In the social reward task, the face was paired directly with 1 brush stroke. In the incentive reward task, directly after the face presentation a smiley face appeared or did not appear, and the participant responded with the space bar. A running total of tickets won was presented across trials. In the uncertainty condition, the popping noise sounded at a jittered interval following the presentation of the face (.5'' or 1''). An example of the four trial types (of the brush task) is displayed in Figure 8.

Figure 8.



Measures

Demographics. In addition to age, gender, and race, participants reported the highest level of education completed by their mothers and fathers. Parental educational attainment is a commonly used gauge of socioeconomic status (SES; Bradley & Corwyn, 2002) and believed to be a more stable and accurate indicator than family income, which may be confounded by family structure, the number of working parents in two-parent families, temporary episodes of unemployment, etc. Educational attainment was coded on an 8-point ordinal scale ranging from "grade school or less" to "finished graduate or professional school." Age, gender, race, and SES were included as covariates in final models.

Environmental Experiences.

Parental Bonding Instrument (PBI). The PBI includes 25-items measuring the quality of attachment bonds between primary caregivers and child. The protection subscale (13 items) captures over involvement from parents, and the care subscale (12 items) assesses level of parent affection and nurturance. The combination of these two subscales reflects the level of optimal, healthy bonding between parent and child. The combined dimensions reflect the level of negligent parenting (low care and low protection), affectionless control (low care and high protection), affectionate constraint (high protection and high care) and optimal parenting (high care and low control). The participant is instructed to rate the attitudes and behaviors of their primary caregiver as remembered in the first 16 years of life. Subjects score their statements about their primary caregiver on a four-point Likert-type scale, from '1' (very like) to '4' (very unlike). The PBI demonstrates long-term stability, and is not affected by mood states or recent life experiences (Wilhelm, Niven, Parker, & Hadzi-Pavlovic, 2005).

Risky Families Questionnaire (RSQ). The RSQ assesses childhood adversity (Taylor, Lerner, Sage, Lehman, & Seeman, 2004) with 13 items asking the extent to which the respondent felt loved and cared for; was insulted; was verbally or physically abused; and observed violence or fighting between family members. Item responses ranging from '1' (not at all) to '5' (very often). The self-report measure is highly correlated with ratings from clinical interviews (Taylor et al., 2004). Two subscales were constructed by item means to reflect family adversity (6 items) and family enrichment and resources (3 items).

Social and Personality Traits.

Barratt Impulsiveness Scale (BI). The BI includes 30 items capturing attention, motor and non-planning components of impulsiveness. Participants rate the frequency in which their behavior or thoughts match each statement, from '1 (rarely/never) to '4' (almost always/always). Items are averaged such that higher scores indicate higher impulsiveness. The nonplanning subscale was also used in the construction of the constraint principle component (see below).

Brief Sensation Seeking Scale (BSSS). The BSSS includes eight items capturing a proclivity for seeking thrilling and exciting experiences, such as liking to explore strange places and wanting to try bungee jumping. Items are rated from '1' (strongly disagree) to '5' (strongly agree) and the average score is computed.

Difficulties in Emotion Regulation Scale (DERS). The DERS captures perceptions in the level of difficulty in regulating negative emotions with 36 items assessing multiple facets of emotion regulation (Gratz & Roemer, 2004). These subscales include non-acceptance of emotions, difficulties with goal-oriented behavior when upset, difficulties in controlling oneself when upset, deficits in emotional awareness, absence of strategies to regulate emotions, and lack of emotional clarity. Participants rate how often statements apply to them on a scale from '1' (almost never) to '5' (almost always), and a sum of 36 items is taken.

Multidimensional Personality Questionnaire (MPQ). The short version of the MPQ includes 155 items tapping into the following trait scales: Wellbeing, Social Potency, Achievement, Social Closeness, Stress Reaction, Aggression, Alienation, Control, Harm avoidance, Traditionalism, and Absorption. These trait scales load into four higher-order factors including positive emotionality (PEM), negative emotionality (NEM), constraint (CON), and absorption (ABS) (Cain et al., 2015). For the current analysis, individual subscales were used to select the most highly correlated subscales for each of the intended traits relevant to reactivity to social reward (sociality), incentive reward (impulsive approach), and stress (stress reactivity). Participants choose true or false to statements based on whether the statement applies to them, or select 1 of 2 statements that best describes them, and the average for each subscale is computed.

Analytical Plan

To accomplish the aims outlined above, a number of steps were necessary to arrive at final measures of momentary reactivity/threshold and emotional learning/reflection for specific emotional systems and constraint, as well as final gauges of environmental quality and personality traits relevant to emotional reactivity. Specifically, these steps of data reduction condense the multiple experimental and survey measures gathered from the procedures above to create a subset of indices that account for maximum variation in the data. For quantification of momentary reactivity/threshold, participants' measures of momentary responses to varying intensities of the same stimulus were entered in a mixed model for repeated-measures using the lme4 package in R in order to extract individual intercepts (baseline ratings of the lowest intensity of social reward, incentive reward, and uncertainty) and slopes (rate of increase in ratings with increasing levels of intensity). Second, emotional learning was quantified by computing 1) maximum rating of the CS+ across trials, 2) speed of which participant reached his or her peak score (trial with the maximum rating), and 3) difference score between the average ratings of CS + across all trials after the initial trial and average ratings of CS- across the same trials. Final experimental sensitivity indices for each emotional system were selected based on visual inspection of data, variability of indices, and the correlation between threshold measures and conditioning, as threshold of response to each emotional cue should theoretically and practically be related to strength of conditioning. Second, to create final measures of general sensitivity, environmental quality, and personality traits, principle component analysis (PCA) was employed. PCA is a means of reducing correlated observed variables to a set of independent composite variables that account for maximal variability in the data. All variable distributions were normalized and fully standardized prior to the PCA calculation as nonnormal distributions and unscaled data can bias PCA results. PCA was performed using the prcomp package in R. Third, for the final test of hypotheses, including environmental effects on sensitivity, and effects of sensitivity and environment on personality traits, four structural equation models (modeling social reward, incentive reward, stress reactivity, and constraint) were estimated using full information maximum likelihood within the lavaan package in R.

Results

Experimental Quantification of Sensitivity (Aim 1)

Descriptive statistics for experimental measures and the estimates of individual slopes and intercepts for momentary reactivity to social reward (brush), incentive reward (tickets), and stress (uncertainty) are displayed in Table 1. The steps taken to identify best indices of momentary reactivity, propensity to condition, and to initially assess the association between momentary reactivity and conditioning are described below.

Momentary Reactivity. Boxplots of the distributions of momentary reactivity ratings to soft touch, incentive reward, and uncertainty are displayed in Figures 9-11. Increases in levels of each emotional cue correspond with incremental increases in ratings of emotional feelings. For quantification of momentary reactivity/threshold, participants' measures of momentary responses to varying intensities of the same stimulus were entered in a repeated-measures mixed model. This allowed for extraction of individual intercepts (baseline ratings of the lowest intensity of social reward, incentive reward, and uncertainty) and slopes (rate of increase in ratings with increasing levels of intensity). Visual inspection of scatterplots among all experimental variables (raw ratings and extracted intercepts and slopes) for each emotional cue (Figure 12) indicated that baseline momentary reactivity (intercepts) were strongly related to conditioning difference scores (difference between average ratings of CS+ and CS-) and to the maximum rating of the CS+ across conditioning trials. For momentary ratings of social and incentive reward, the intercept was substantially more informative than the slope. Visual inspection of individual trajectories suggest that a majority of participants reach their 'peak' in ratings of reward at the low intensity level, which explains the reduced mean slope values of reward relative to the uncertainty slope. The slope for uncertainty momentary ratings, unlike reward slopes, was also strongly related to conditioning indices. These four measures of momentary reactivity (all three intercepts and uncertainty slope) were retained for final models.

Conditioning. Associative conditioning is successful when the difference score between average ratings of the CS+ and average ratings of the CS- (after the first trial) is above zero. A graphical display of ratings across trials to the CS+ and CS- collapsed across all individuals, for only individuals who conditioned, and for only individuals who did not condition across the three emotional cues is shown in Figure 13. At the whole group level, the uncertainty condition led to the strongest divergence between ratings of CS+ and CS-, followed by incentive reward and finally social reward. Divergence is more prominent in those that did condition, and the CS+ and CS- ratings remain indistinguishable for non-conditioners. As shown in Figure 12, maximum rating of the CS+ during conditioning had slightly stronger relations to momentary reactivity than difference scores, and was highly correlated with difference scores, so maximum ratings were used in final models as the index for conditioning.

Relationship between Momentary Reactivity and Conditioning. The relationships between momentary reactivity ratings and conditioning are displayed in Figures 14 and 15. First, Figure 14 shows the differences in divergence in ratings between CS+ and CS- for those with low, mean, and high momentary ratings (using the intercept for social and incentive reward and the slope for uncertainty). There is a clear association between the strength of momentary responses and difference in ratings of the CS+ relative to the CS- across trials. Second, Figure 15 displays the associations between momentary reactivity ratings for each level of the emotional cue and the peak CS+ rating. These associations suggest that the strength of momentary emotional responses are related to downstream depth of processing of the cue and its associated context, as predicted by the model.

Momentary Reactivity and Conditioning Collapsed Across Emotional Systems. Neural constraint as represented in the model exerts modulation across all emotional systems. Therefore, momentary reactivity and conditioning across systems within an individual is of interest to capturing general sensitivity scores that might relate to constraint. Figures 16-18 display momentary reactivity ratings (for baseline levels of intensity [1 brush stroke, 1 ticket, and 0% probability; Figure 16] and mid-levels of intensity [2 brush strokes, 2 tickets and 50% probability; Figure 17]), and conditioning difference scores (Figure 18) across emotional systems. Figures 16 and 17 show a slight positive trend in momentary ratings, such that individuals tend to increase in momentary ratings across more than one task. Figure 18 shows that across emotional systems for conditioning differences scores, there is a rather large cluster of individuals who do not condition across the three emotional tasks, with others 'fanning out' in conditioning propensity. Minimal individuals demonstrate very high difference scores across all three systems. Given the large cluster of individuals with very low conditioning across tasks, these individuals were classified as 'non-conditioners' if their difference scores were below 5% of the scale for all emotional systems (*n* = 45; 11% of sample).

To potentially capture general modulation across systems, principle components were created from the three measures of momentary reactivity across emotional systems (slope for uncertainty and intercepts for social and incentive reward), and from three measures of conditioning (maximum rating). The resulting components represent 'general sensitivity', in terms of 1) momentary reactivity to emotional cues and 2) emotional learning to both rewards and stressors. The scales and their loadings for all calculated components are displayed in Table 3 below. Conditioners and nonconditioners show drastic differences in the conditioning component (as would be expected), and because conditioning occurs on a continuous scale, the component is used to assess general conditioning propensity in final models rather than the categorical variable. Final models and visual inspections address differences between conditioners and nonconditioners, and the general sensitivity components in more detail below.

Table 1: Descriptive Statistics for Experimental Measures of Sensitivity

Variable	n	mean	sd	range
Momentary Reactivity/Threshold Measures				
Brush1	371	52.68	21.48	100
Brush2	371	57.76	21.13	100
Brush3	371	61.2	22.08	100
Ticket1	388	48.18	23.59	100
Ticket2	388	53.26	23.59	100
Ticket3	388	57.76	23.59	100
Ticket4	388	61.63	24.36	100
Pop0	392	10.24	16.06	86
Pop25	392	32.76	19.93	91
Pop50	392	42.9	21.39	91
Pop75	392	46.58	24.97	97.5
Pop100	392	43.26	28.14	100
Emotional Learning/Reflection Measures				
Brush Difference	393	6.19	15.34	133.67
Ticket Difference	391	16.55	20.43	128.11
Pop Difference	389	28.17	23.92	103.5
Brush Max	393	41.16	24.5	100
Ticket Max	391	47.62	27.65	100
Pop Max	389	61.32	27.16	100
Brush Peak Trial	393	5.36	2.92	8
Ticket Peak Trial	391	6.49	2.87	8
Pop Peak Trial	389	4.15	1.8	5
Repeated Measures Individual Estimates				
Brush Intercept	371	48.73	19.41	94.39
Brush Slope	371	4.24	2.21	15.52
Ticket Intercept	388	43.43	23.26	97.43
Ticket Slope	388	4.81	3.86	29.78
Pop Intercept	392	3.31	8.14	51.94
Pop Slope	392	11.92	5.08	23.2

Figure 9

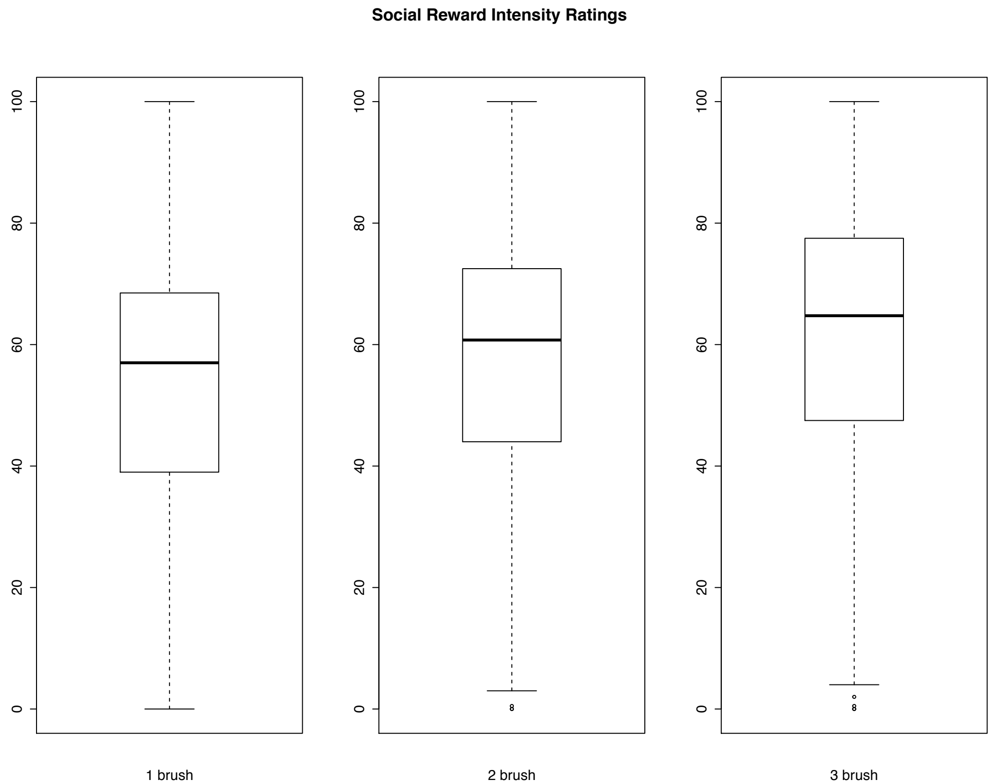

Social Reward Intensity Ratings
0
20
40
60
80
100
1 brush
2 brush
3 brush

Figure 10

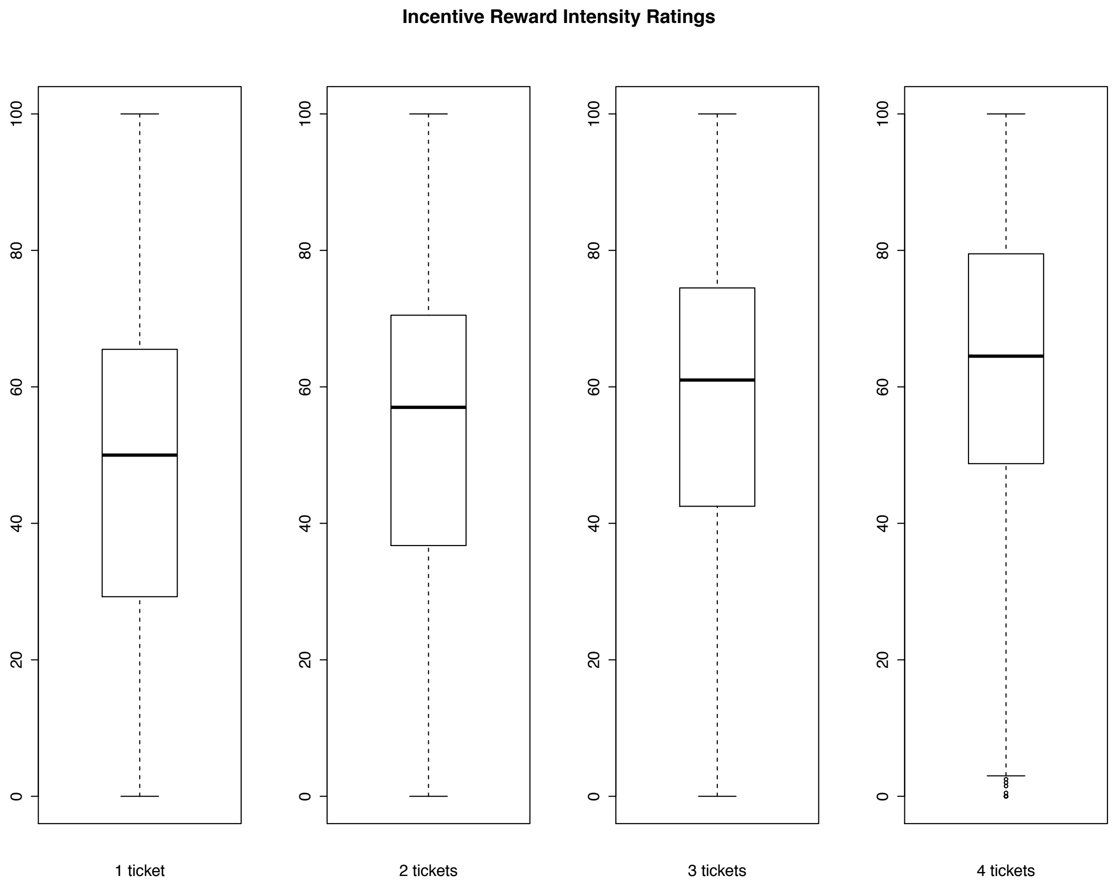

Incentive Reward Intensity Ratings
0
20
40
60
80
100
1 ticket
2 tickets
3 tickets
4 tickets

Figure 11

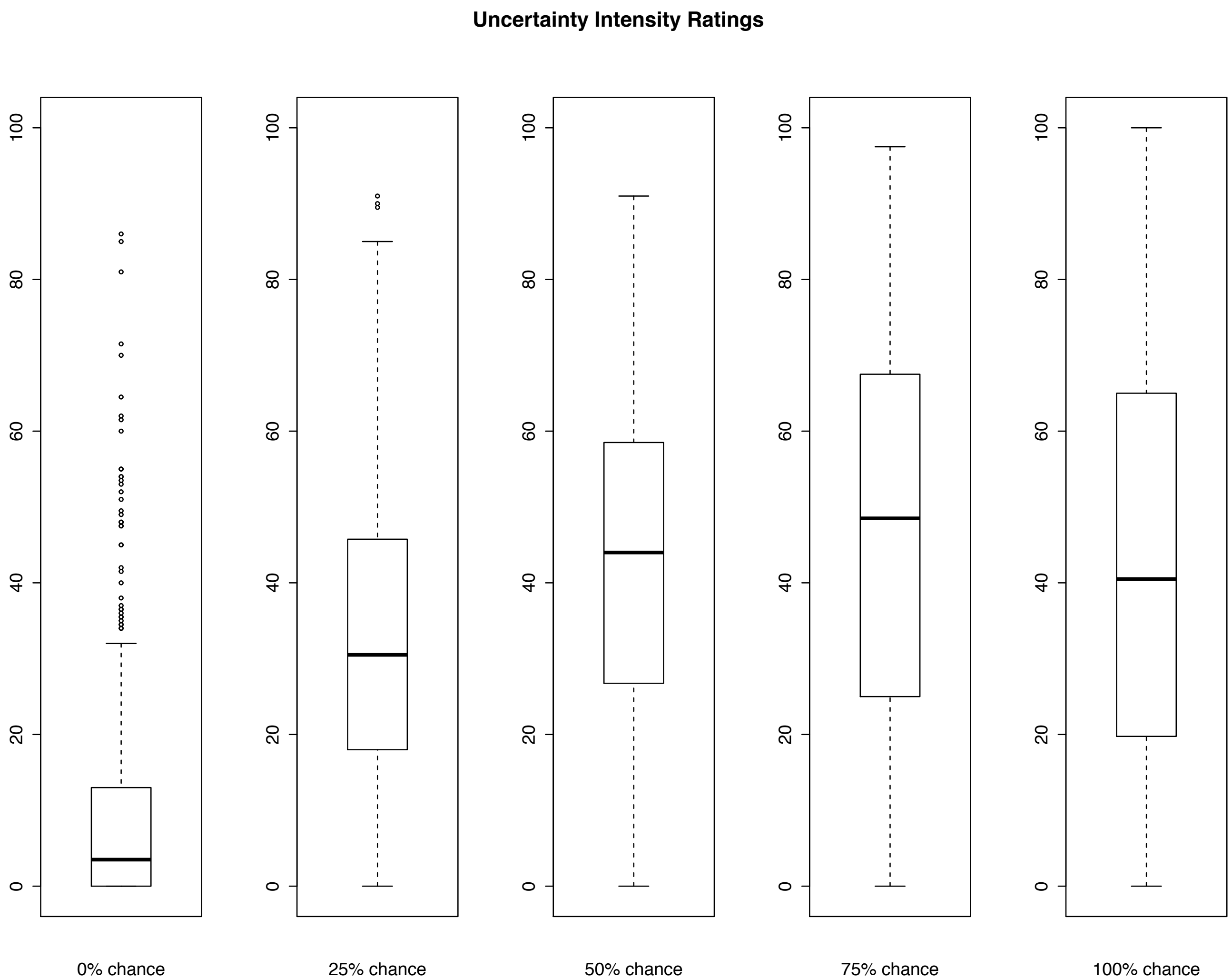

Uncertainty Intensity Ratings
100
80
60
40
20
0
0% chance
25% chance
50% chance
75% chance
100% chance

Figure 12.

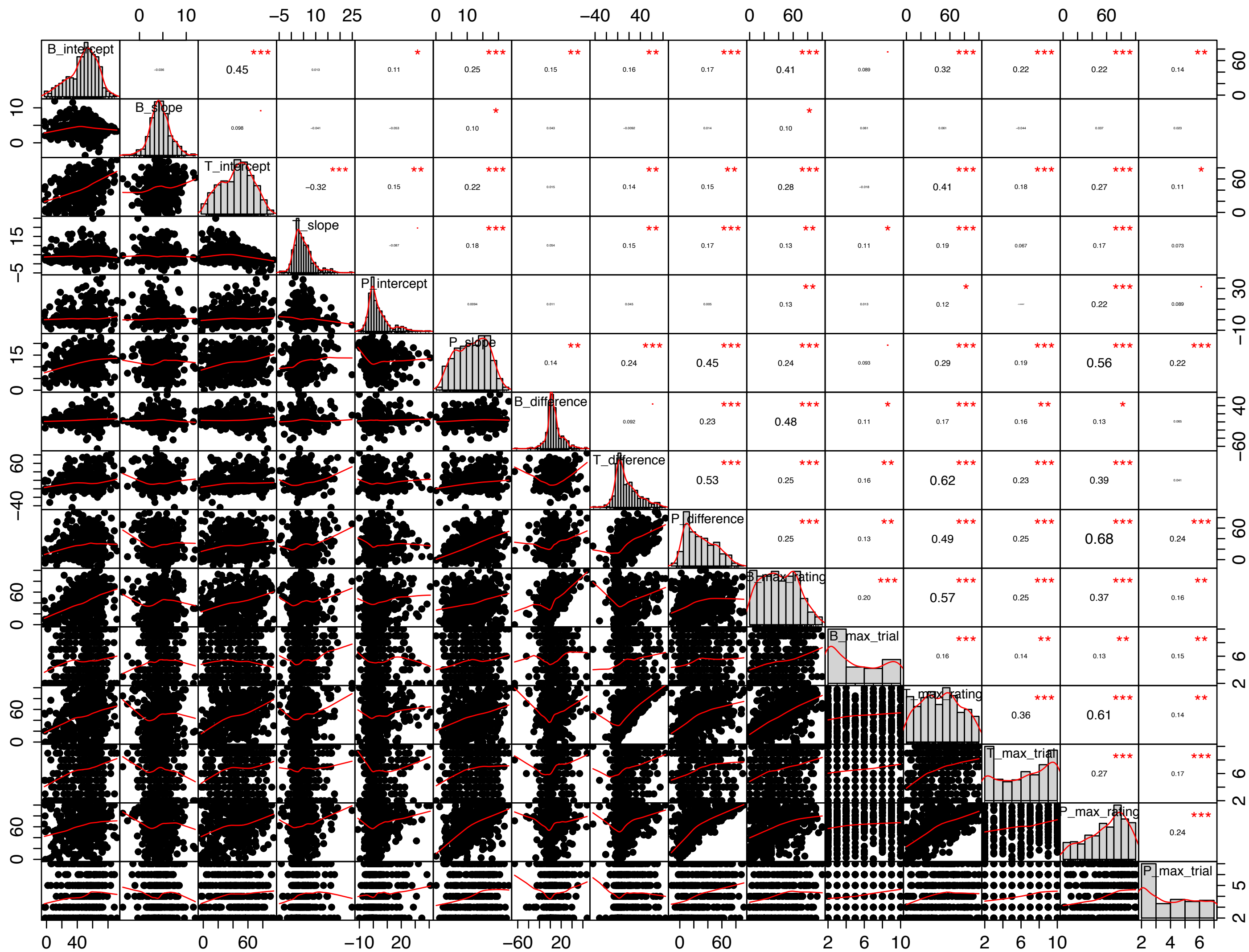

B_intercept
B_slope
T_intercept
T_slope
P_intercept
P_slope
B_difference
T_difference
P_difference
B_max_rating
B_max_trial
T_max_rating
T_max_trial
P_max_rating
P_max_trial

Figure 13.

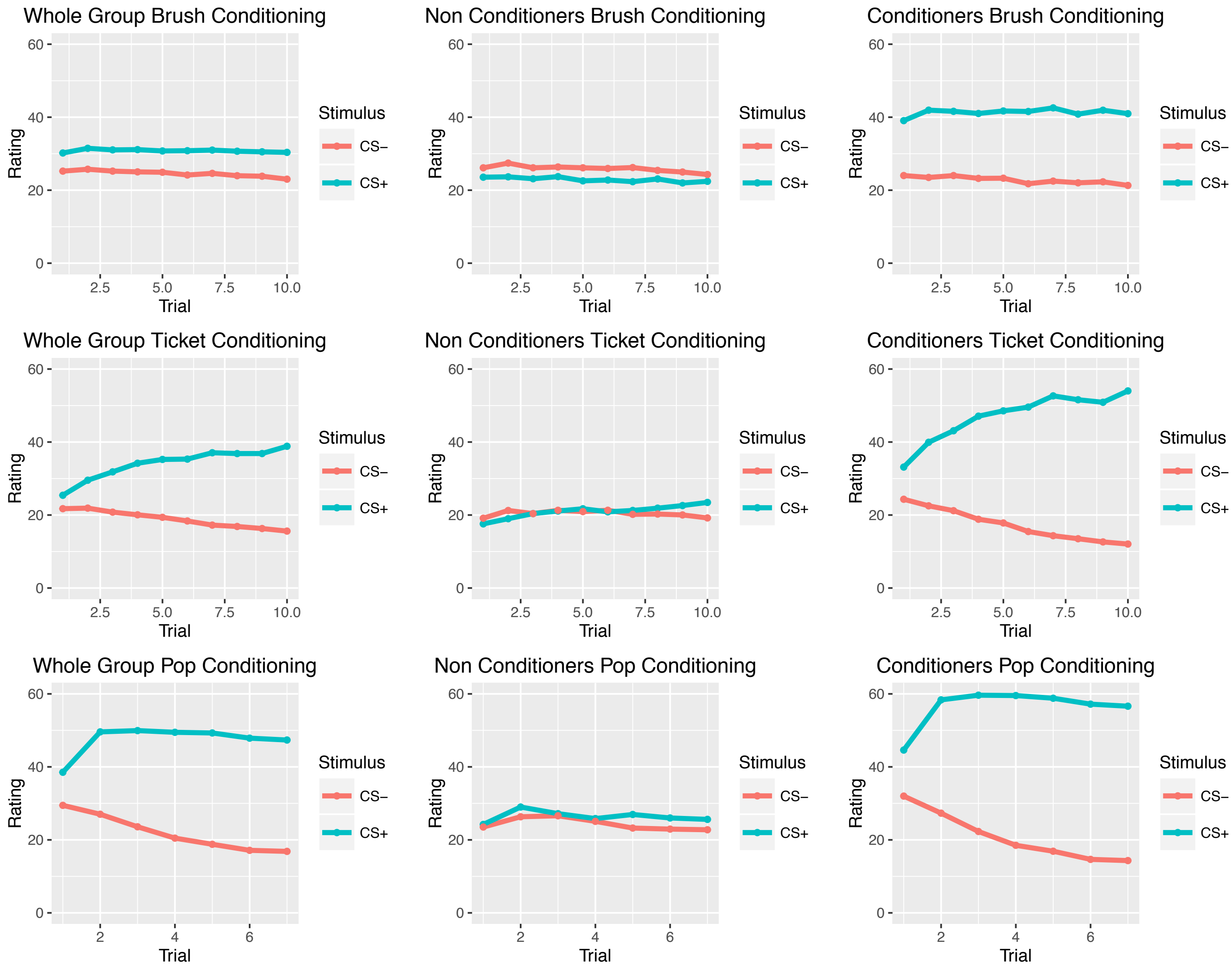

Whole Group Brush Conditioning
Non Conditioners Brush Conditioning
Conditioners Brush Conditioning
Whole Group Ticket Conditioning
Non Conditioners Ticket Conditioning
Conditioners Ticket Conditioning
Whole Group Pop Conditioning
Non Conditioners Pop Conditioning
Conditioners Pop Conditioning
Rating
Trial
Stimulus
CS–
CS+
0
20
40
60
2.5
5.0
7.5
10.0
2
4
6

Figure 14.

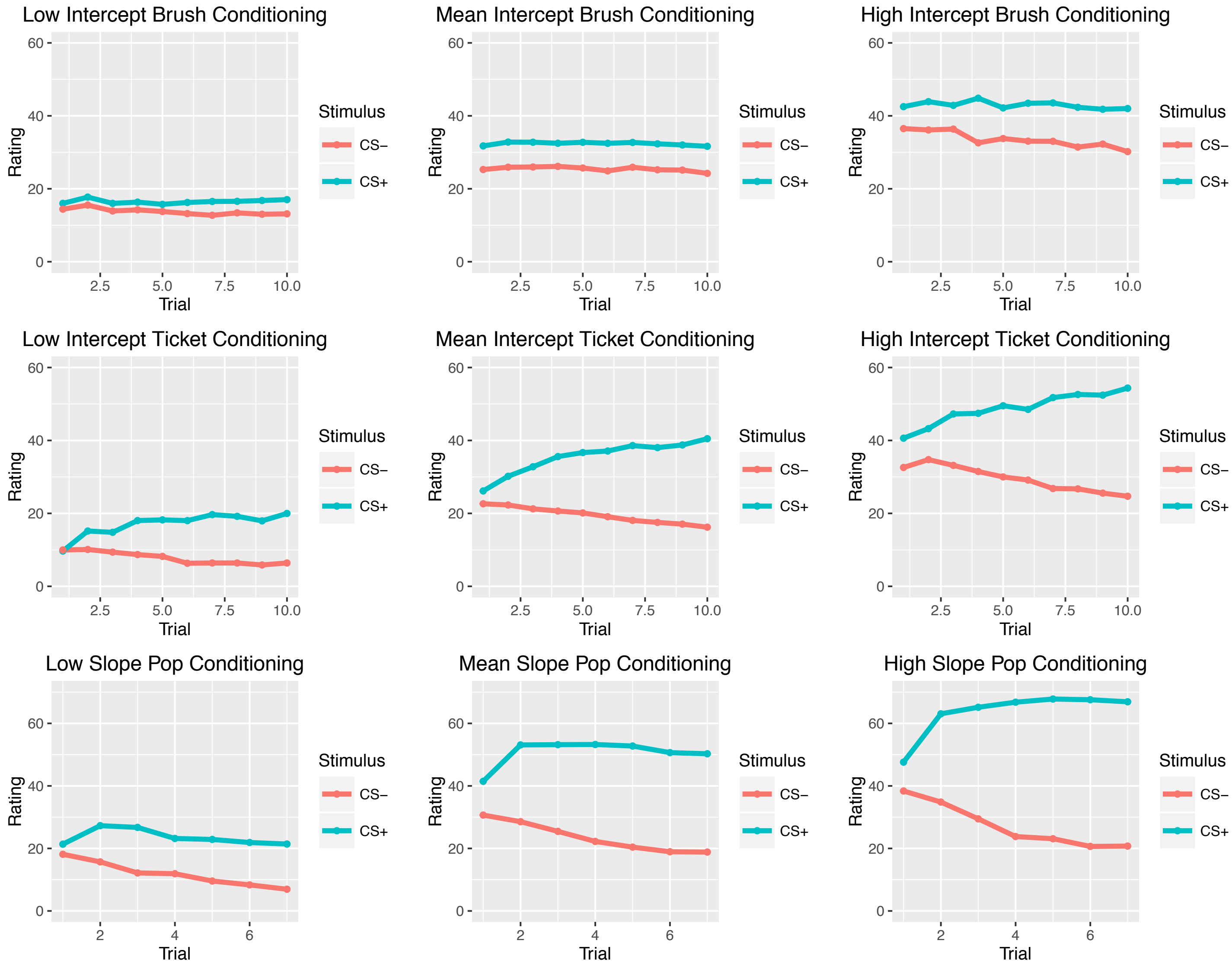

Low Intercept Brush Conditioning
Mean Intercept Brush Conditioning
High Intercept Brush Conditioning
Low Intercept Ticket Conditioning
Mean Intercept Ticket Conditioning
High Intercept Ticket Conditioning
Low Slope Pop Conditioning
Mean Slope Pop Conditioning
High Slope Pop Conditioning
Rating
Trial
Stimulus
CS−
CS+

Figure 15.

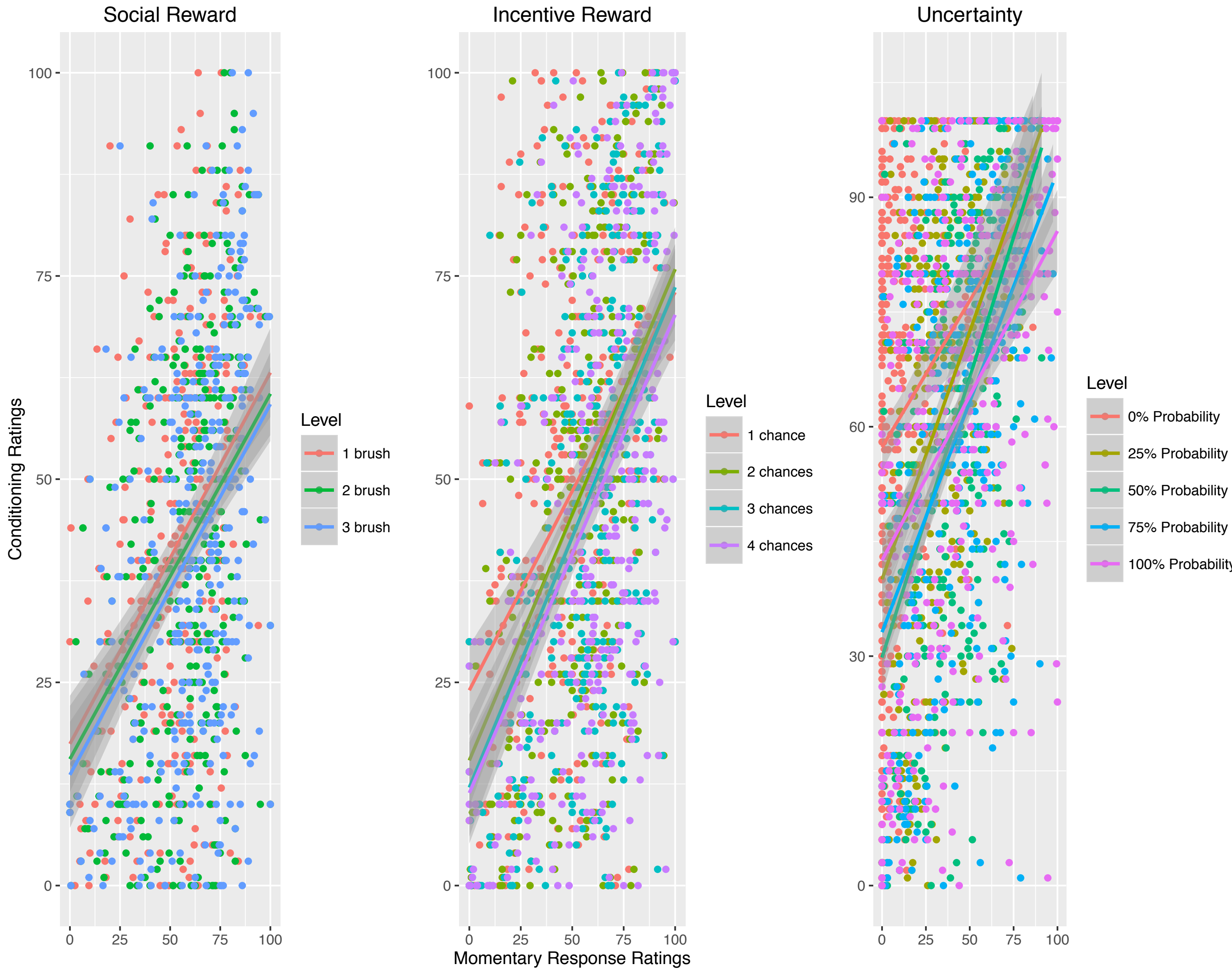

Social Reward
Incentive Reward
Uncertainty
Conditioning Ratings
Momentary Response Ratings
Level
1 brush
2 brush
3 brush
Level
1 chance
2 chances
3 chances
4 chances
Level
0% Probability
25% Probability
50% Probability
75% Probability
100% Probability
0
25
50
75
100
0
30
60
90

Figure 16.

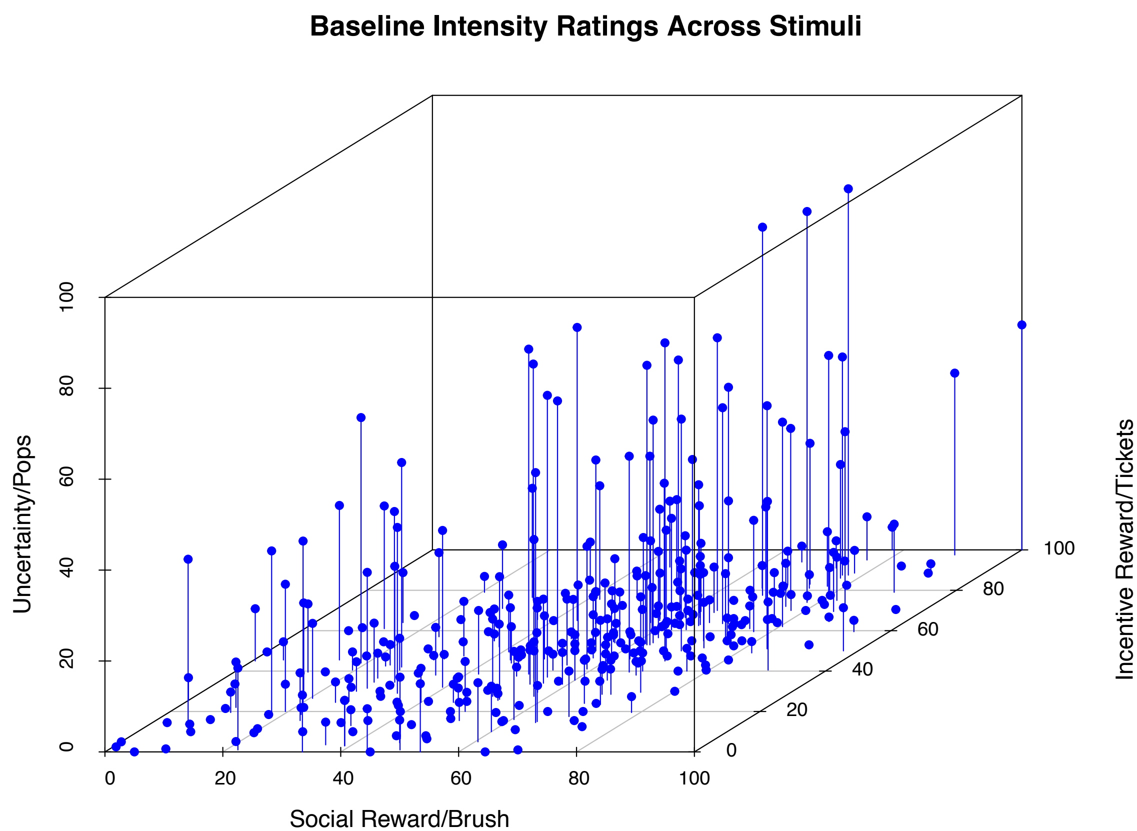

Baseline Intensity Ratings Across Stimuli
Uncertainty/Pops
0
20
40
60
80
100
Social Reward/Brush
0
20
40
60
80
100
Incentive Reward/Tickets
0
20
40
60
80
100

Figure 17.

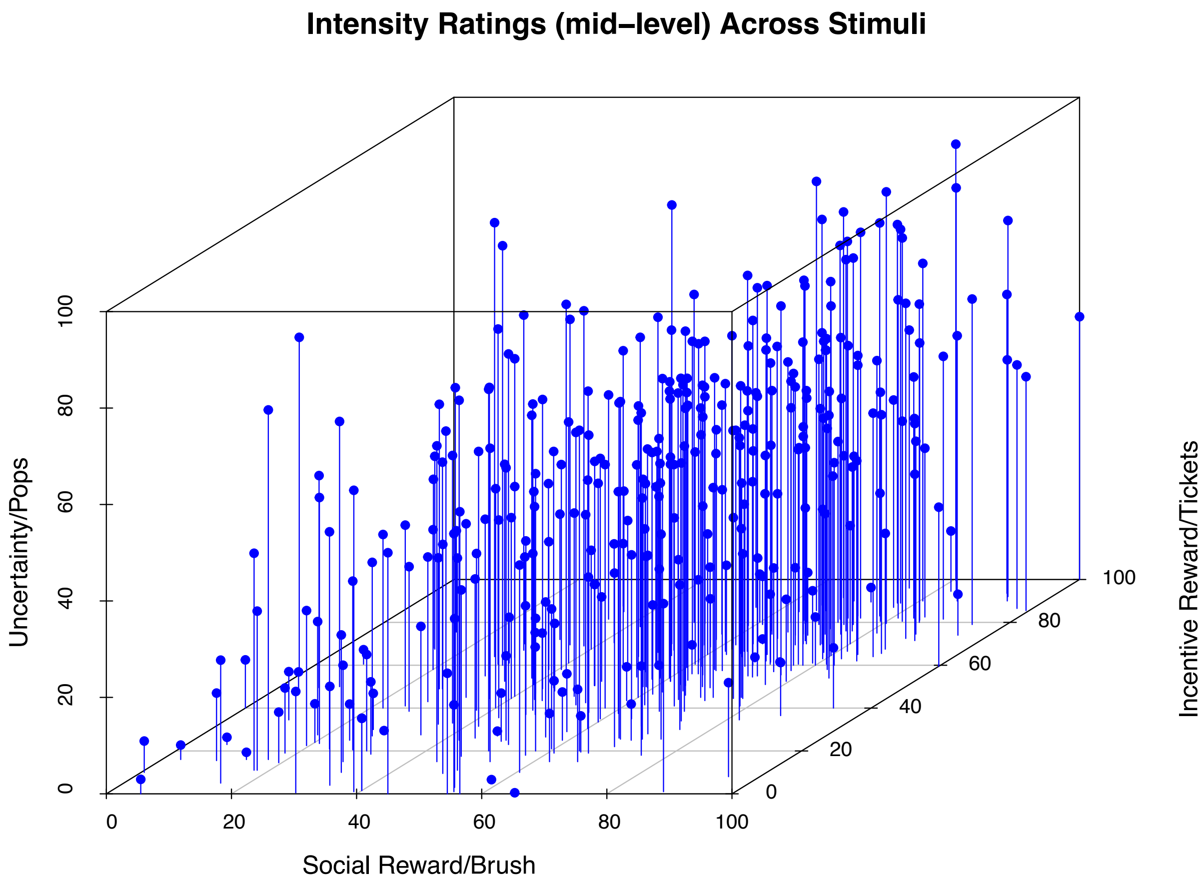
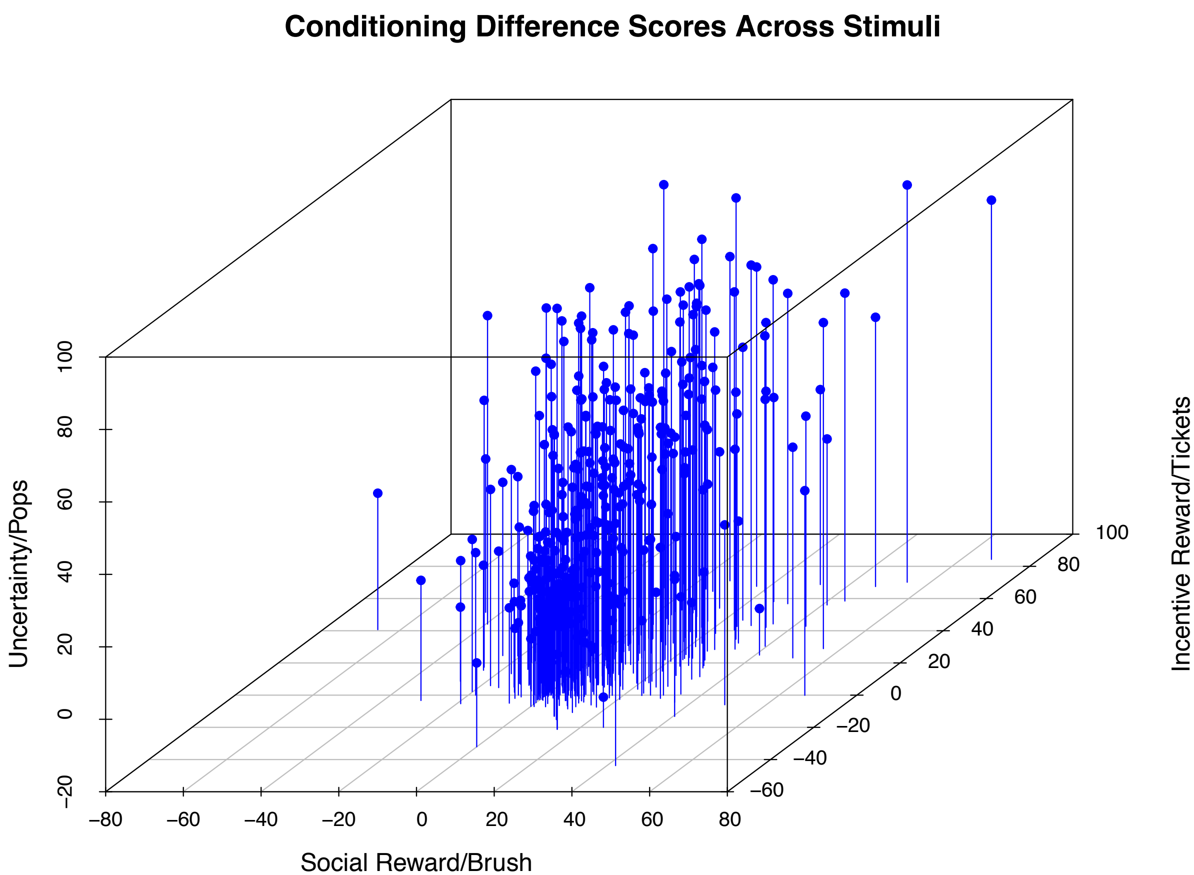

Intensity Ratings (mid–level) Across Stimuli
Uncertainty/Pops
0
20
40
60
80
100
Social Reward/Brush
0
20
40
60
80
100
Incentive Reward/Tickets
0
20
40
60
80
100

Figure 18.


Conditioning Difference Scores Across Stimuli
Uncertainty/Pops
−20
0
20
40
60
80
100
Social Reward/Brush
−80
−60
−40
−20
0
20
40
60
80
Incentive Reward/Tickets
−60
−40
−20
0
20
40
60
80
100

Environmental Predictors of Sensitivity (Aim 2)

PCA Data Reduction. Environmental (and personality) measures from the survey were selected based on degree of correlation in the data to create composite measures. Descriptive statistics for all survey measures and correlations among variables are displayed in Table 2. Principle components reflecting environmental quality were calculated from the four environmental subscales (care, overprotection, adversity, and enrichment).

To verify that components were stable across PCAs, random subsets of $n = 200$ were taken from the data and the PCAs were recalculated. The first components were stable in all cases, and were used in final analyses. For environmental measures, the second component was also stable, and retained for analyses to ensure that environmental factors were adequately accounted for in final models. A display of these two environmental components is displayed in Figure 19. The first (PC1) represents general environmental quality, ranging from highly adverse, unsafe, and abusive (low scores), to highly enriched, safe, and nurturing (high scores). The second (PC2) captures parent overprotection, or intrusive and excessive parenting (high scores).

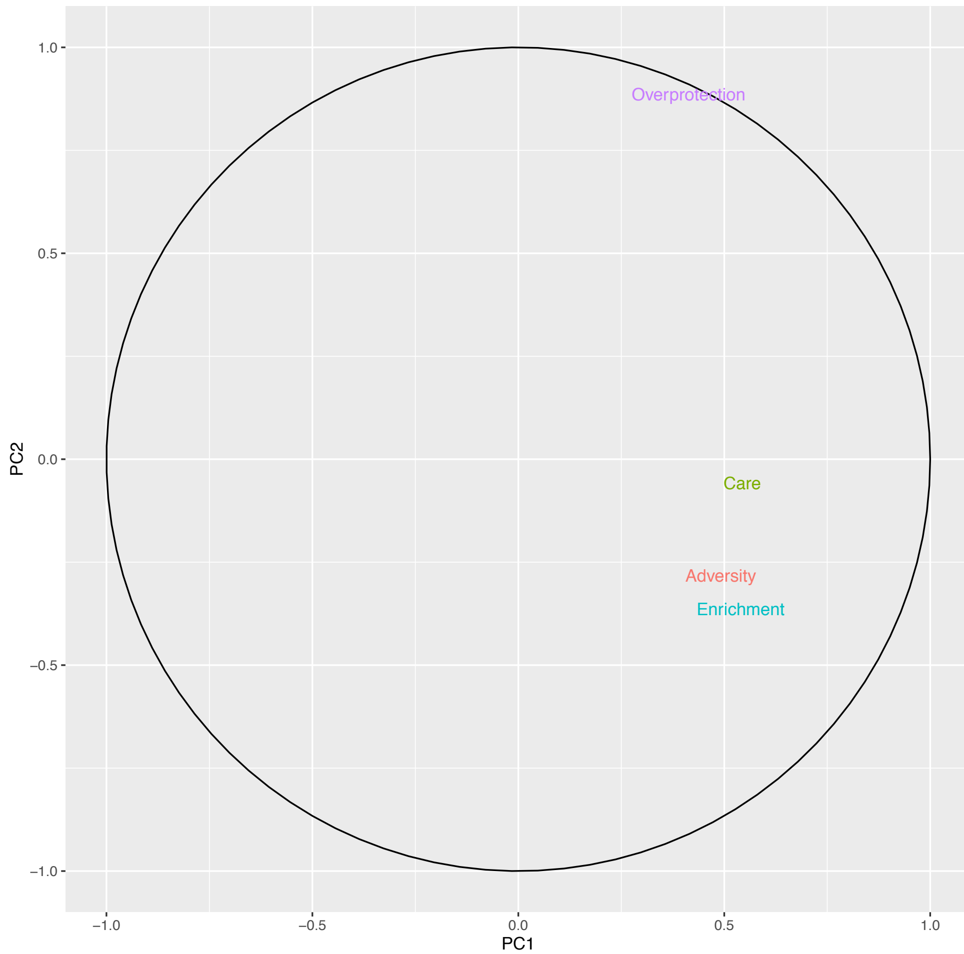
Table 2: Descriptive Statistics and Correlations of Survey Variables

	n	mean	sd	Care	Overprotection	Nonplanning	DERS	Adversity	Enrichment	Sensation Seeking	Well Being	Social Potency	Achievement	Social Closeness	Stress Reactivity	Alienation	Control	Harm Avoidance
Care	407	1.59	0.56															
Overprotection	407	2.86	0.59	-0.46														
Nonplanning	404	2.08	0.43	0.18	-0.12													
DERS	407	87.02	21.09	0.28	-0.26	0.24												
Adversity	408	9.44	3.99	0.55	-0.34	0.23	0.3											
Enrichment	408	4.26	0.8	-0.76	0.36	-0.2	-0.25	-0.56										
Sensation Seeking	408	3.26	0.77	0.06	-0.06	0.25	0.08	0.17	-0.03									
Well Being	406	1.42	0.22	0.2	-0.19	0.1	0.34	0.11	-0.22	-0.23								
Social Potency	406	1.48	0.26	0.09	-0.17	0.09	0.18	0.02	-0.11	-0.21	0.37							
Achievement	406	1.31	0.27	0.04	-0.1	0.45	0.11	0	-0.07	-0.03	0.24	0.24						
Social Closeness	406	1.35	0.27	0.22	-0.13	0	0.27	0.14	-0.24	-0.22	0.29	0.3	0.06					
Stress Reactivity	406	1.61	0.27	0.16	-0.18	0.15	0.59	0.22	-0.16	0	0.3	0.21	0.01	0.24				
Alienation	406	1.74	0.21	-0.27	0.23	-0.21	-0.36	-0.37	0.24	-0.09	-0.08	-0.06	0.02	-0.29	-0.41			
Control	406	1.29	0.18	0.07	-0.01	0.5	0.12	0.17	-0.1	0.34	0.01	-0.09	0.34	-0.09	0.03	-0.03		
Harm Avoidance	406	1.32	0.21	0.15	-0.07	0.23	0.07	0.14	-0.08	0.39	-0.02	-0.01	0.02	0.06	0.08	-0.07	0.3	
Impulsivity	406	2.06	0.34	0.14	-0.13	0.77	0.32	0.24	-0.13	0.35	0.03	0.02	0.37	0	0.24	-0.22	0.52	0.31

Table 3: PCA Results

Survey Measures			Experimental Measures	
Positive Emotionality			Momentary Reactivity	
Well Being	-0.59		Brush Intercept	-0.63
Social Potency	-0.59		Ticket Intercept	-0.62
Social Closeness	-0.55		Pop Slope	-0.48
% of variation	54		% of variation	55
Negative Emotionality			Conditioning	
DERS	-0.6		Brush Max	0.54
Stress Reactivity	-0.62		Ticket Max	0.63
Alienation	0.51		Uncertainty Max	0.56
% of variation	64		% of variation	68
Constraint (traditional)				
Control	-0.64			
Harm Avoidance	0.67			
Traditionalism	0.37			
% of variation	45			
Constraint (regulation)				
Nonplanning	0.62			
Achievement	0.55			
Control	0.57			
% of variation	63			
Environment				
	PC1	PC2		
Care	0.54	-0.05		
Overprotection	0.41	0.88		
Adversity	0.49	-0.29		
Enrichment	0.54	-0.36		
% of variation	63	18		

Figure 19. PCA results for Environmental Measures



Relationship Between Early Environment and Sensitivity. The relationships between environmental quality (adverse to enriched) and experimental measures of sensitivity are displayed in Figure 20 (momentary reactivity) and Figure 21 (conditioning). Likewise, the relationships between intrusive parenting and sensitivity are displayed in Figures 22 and 23. Figure 20 demonstrates a positive relationship between environmental quality and momentary reactivity to social and incentive rewards, and mixed relationships between environmental quality and momentary reactivity to uncertainty depending on the level of intensity. At the lowest levels of probability of hearing the aversive noise (0% and 25% probability), there is a negative relationship between care and ratings of anxiety. In contrast, Figure 21 shows minimal differences in conditioning between those who are low, moderate, and high in environmental quality. One potential trend can be observed for individuals reporting low care, where ratings of both the CS+ and CS- decline across trials in the social reward task, suggesting potential discomfort with the soft touch procedure.

For parent overprotection, there are opposite effects in terms of intensity ratings of rewards, displayed in Figure 22. The more overprotection, the lower the responses to social and incentive reward. Relationships between overprotection and anxiety ratings at different probability levels are mixed, with most levels related negatively to overprotection except for a positive relationship between anxiety at 25% probability and overprotection. Figure 23 shows conditioning across trials across levels of parent overprotection. Individuals high in overprotection demonstrate somewhat weaker conditioning to social reward. Levels of overprotection appear unrelated to conditioning to incentive reward and to uncertainty.

Figure 20.

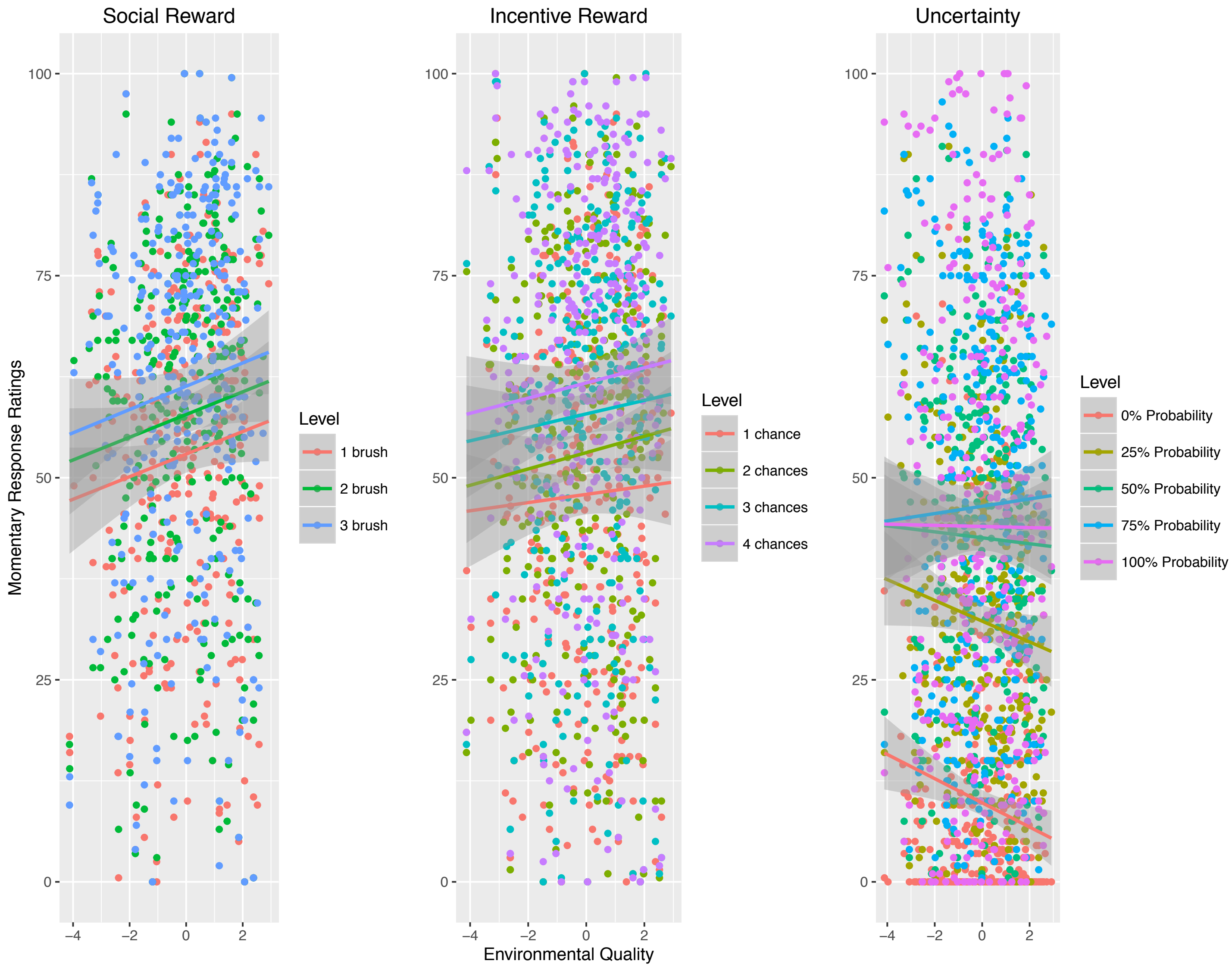

Social Reward
Incentive Reward
Uncertainty
Momentary Response Ratings
Environmental Quality
100
75
50
25
0
−4
−2
0
2
Level
1 brush
2 brush
3 brush
1 chance
2 chances
3 chances
4 chances
0% Probability
25% Probability
50% Probability
75% Probability
100% Probability

Figure 21.

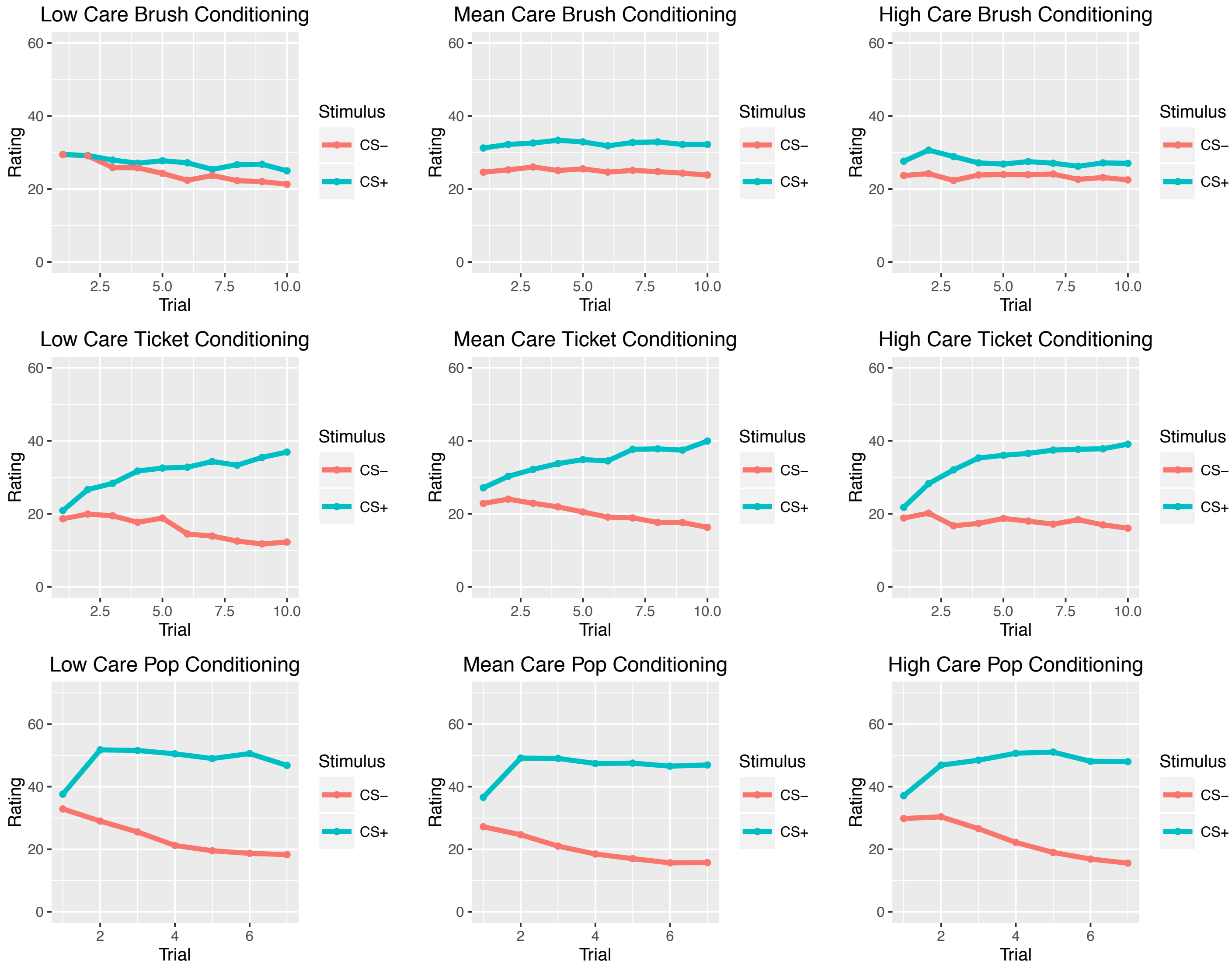

Low Care Brush Conditioning
Mean Care Brush Conditioning
High Care Brush Conditioning
Low Care Ticket Conditioning
Mean Care Ticket Conditioning
High Care Ticket Conditioning
Low Care Pop Conditioning
Mean Care Pop Conditioning
High Care Pop Conditioning
Rating
Trial
Stimulus
CS−
CS+

Figure 22.

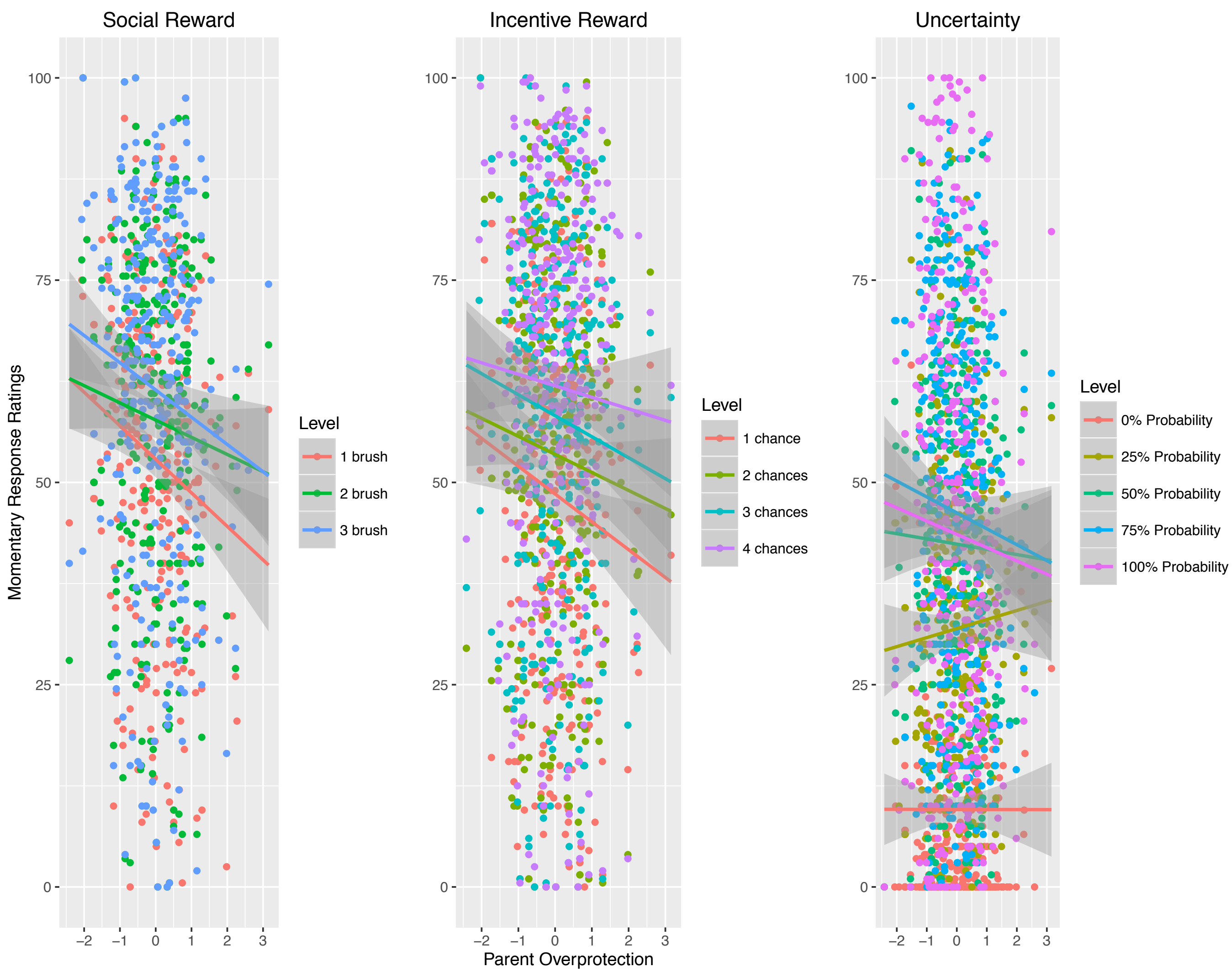
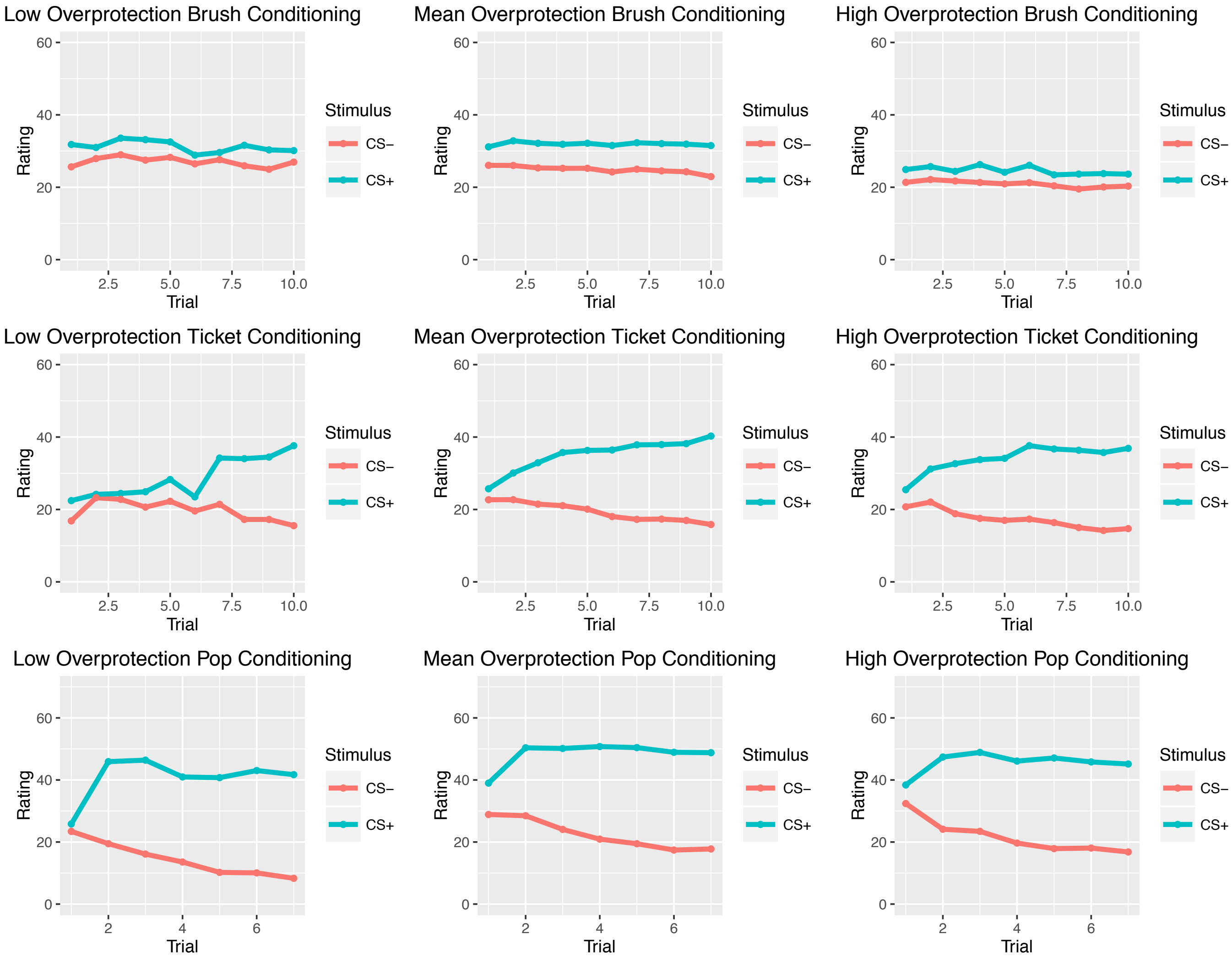

Social Reward
Incentive Reward
Uncertainty
Momentary Response Ratings
Parent Overprotection
100
75
50
25
0
−2
−1
0
1
2
3
Level
1 brush
2 brush
3 brush
Level
1 chance
2 chances
3 chances
4 chances
Level
0% Probability
25% Probability
50% Probability
75% Probability
100% Probability

Figure 23.


Low Overprotection Brush Conditioning
Mean Overprotection Brush Conditioning
High Overprotection Brush Conditioning
Low Overprotection Ticket Conditioning
Mean Overprotection Ticket Conditioning
High Overprotection Ticket Conditioning
Low Overprotection Pop Conditioning
Mean Overprotection Pop Conditioning
High Overprotection Pop Conditioning
Rating
Trial
Stimulus
CS–
CS+
0
20
40
60
2.5
5.0
7.5
10.0
2
4
6

Biology, Environment, and Personality Outcomes (Aim 3)

PCA was applied to condense multiple subscales (see Figures 24-28) into three higher-order traits of interest, including positive emotionality (responsiveness to social situations and tendency towards positive emotions and well being), negative emotionality (reactivity to stressors and tendency to feel upset and anxious), and constraint (planful, goal-oriented, and regulated behavior versus uninhibited, disorganized and impulsive behavior). Positive emotionality typically includes four subscales of the MPQ, including social closeness, social potency, well-being, and achievement. In this sample, achievement did not demonstrate strong correlations with the other subscales, so only three subscales were used in the PCA. Negative emotionality usually includes the stress reactivity, alienation, and aggression MPQ subscales, Aggression was not highly correlated with stress reactivity and alienation, and was replaced instead with the DERS which had strong relations to the other two subscales. Consistent with the MPQ, the resulting components from these two PCAs are termed 'positive emotionality' and 'negative emotionality'.

For the constraint measure, the traditional measures of constraint from the MPQ, including control, harm avoidance, and tranditionalism, were not highly correlated. For this reason, an additional PCA was used to quantify constraint, reflecting higher-level regulation and cognition (including control, achievement and the nonplanning subscale of the BI), which were very highly correlated. Final analyses included both the 'traditional' behavioral constraint component and the 'regulatory' constraint component, and each of these are explored below along with positive and negative emotionality. Figure 29 displays how each of these higher order traits correlates with the standard higher level factor computed by an average of traditionally included subscales of the MPQ.

The relationships between higher level traits computed by PCA and 1) experimental measures of sensitivity and 2) the environment are displayed below in Figures 30-38. Figures 30-33 display how each trait relates to intensity ratings. Positive emotionality positively correlates with ratings in response to social and incentive reward, and negatively relates to ratings of uncertainty. Negative emotionality relates to intensity ratings as well, such that more stress reactive individuals rate report less positive feelings to rewards and more anxiety in response to uncertainty. For the traditional constraint component, constraint relates to higher ratings of anxiety to uncertainty, and lower ratings of positive feelings to reward. The emotion regulation component shows similar but smaller relationships, such that regulation relates to higher anxiety and lower positive feelings to rewards. In terms of general momentary reactivity (the component reflecting intensity ratings collapsed across emotional tasks), there appears to be no relation to higher level traits in Figure 38, except a small positive association with the traditional constraint component.

Ratings across trials in the conditioning procedure for different levels of traits are displayed in Figures 34-37. Ratings across trials of the CS+ in reward and stress conditions for different levels of positive emotionality are similar. Likewise, conditioning appears to be similar across tasks for different levels of negative emotionality. Similar trends are seen for both constraint measures, such that there are no differences in conditioning to social reward, and lower constraint relates to greater conditioning to incentive reward and lower conditioning to uncertainty. Figure 38 shows that the general sensitivity conditioning component relates positively to constraint and regulation, but not other higher order factors.

The relationships between personality traits and environmental measures is also displayed in Figure 38. Environmental quality shows the strongest relationship with negative emotionality, with higher stress reactivity related to lower environmental quality. There are slight trends with positive emotionality and constraint (higher quality environment relates to higher positive emotionality and constraint).

Figure 24.

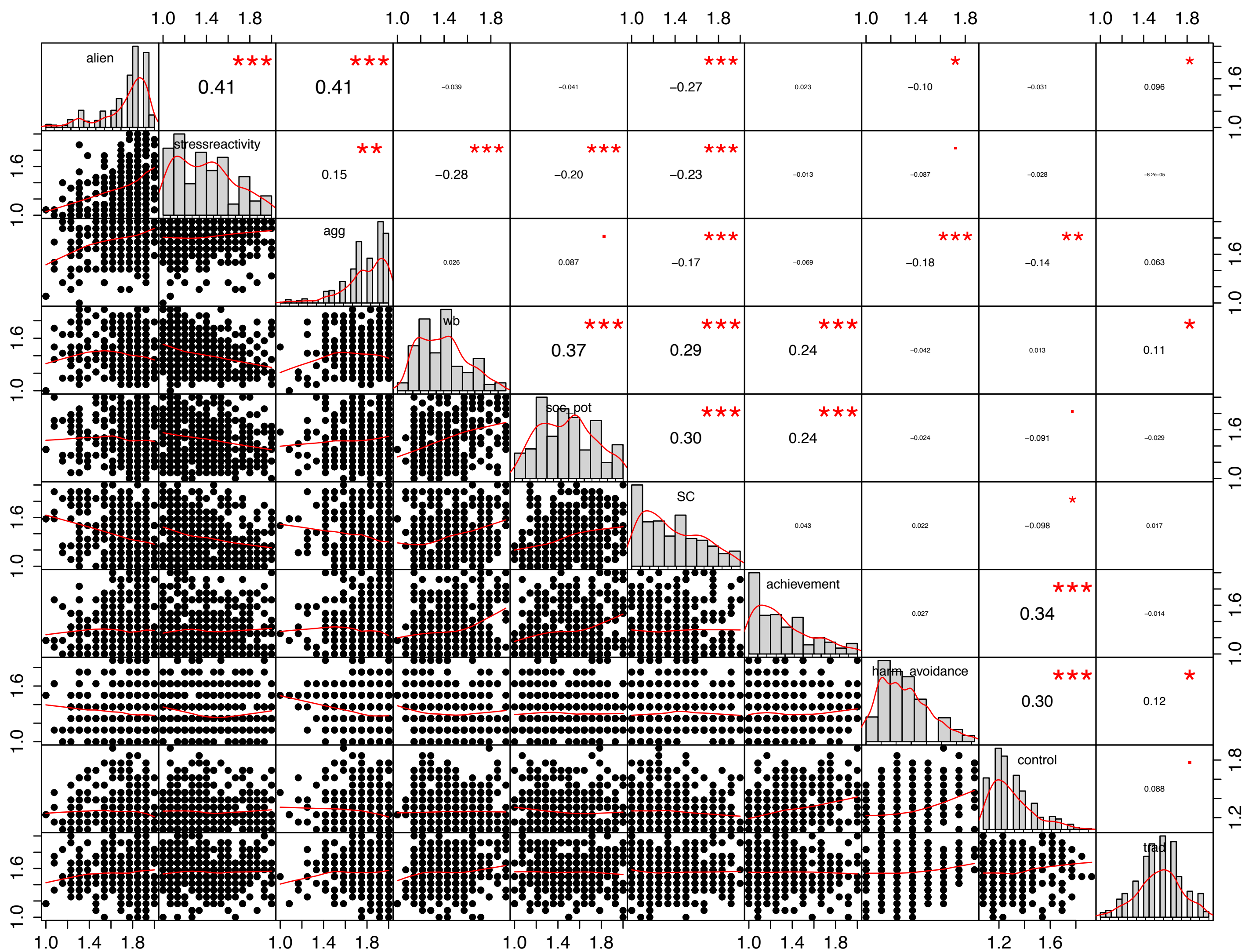

alien
stressreactivity
agg
wb
soc_pot
SC
achievement
harm_avoidance
control
trad
0.41
0.41
0.15
-0.28
-0.20
-0.27
-0.23
-0.17
-0.10
-0.18
-0.14
0.37
0.29
0.24
0.11
0.30
0.24
0.34
0.30
0.12

Figure 25.

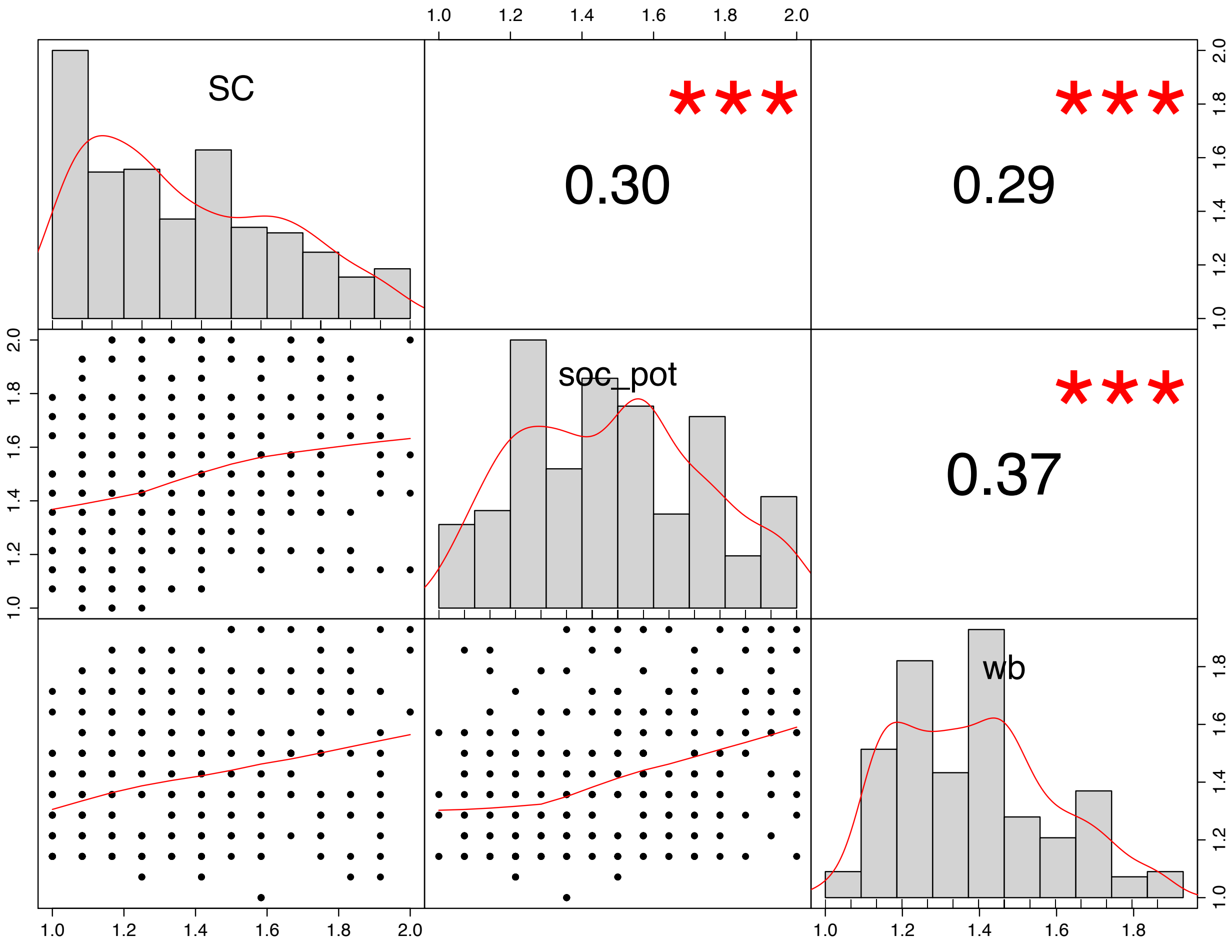


Figure 26.

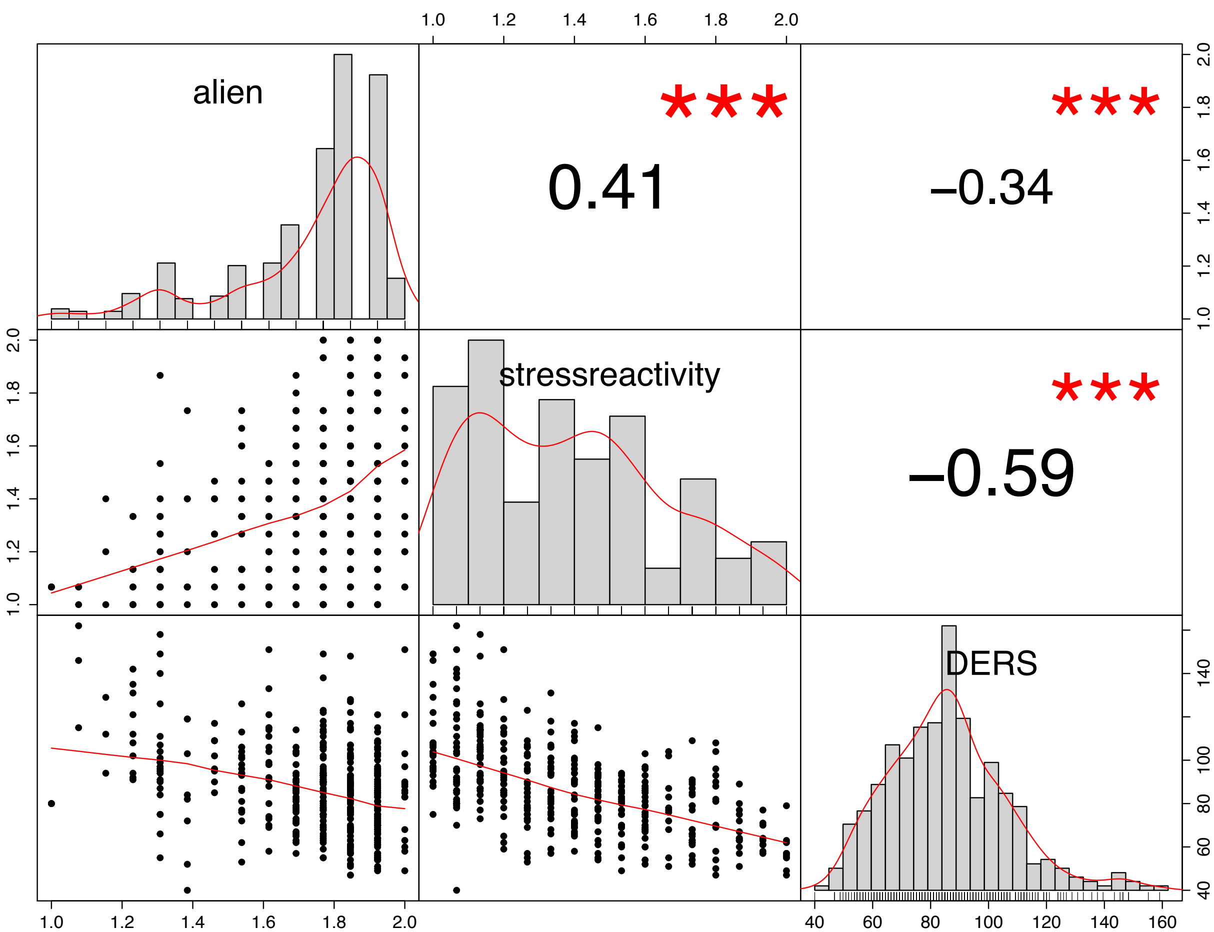

alien
stressreactivity
DERS
0.41
−0.34
−0.59
***
***
***
1.0
1.2
1.4
1.6
1.8
2.0
40
60
80
100
120
140
160

Figure 27.

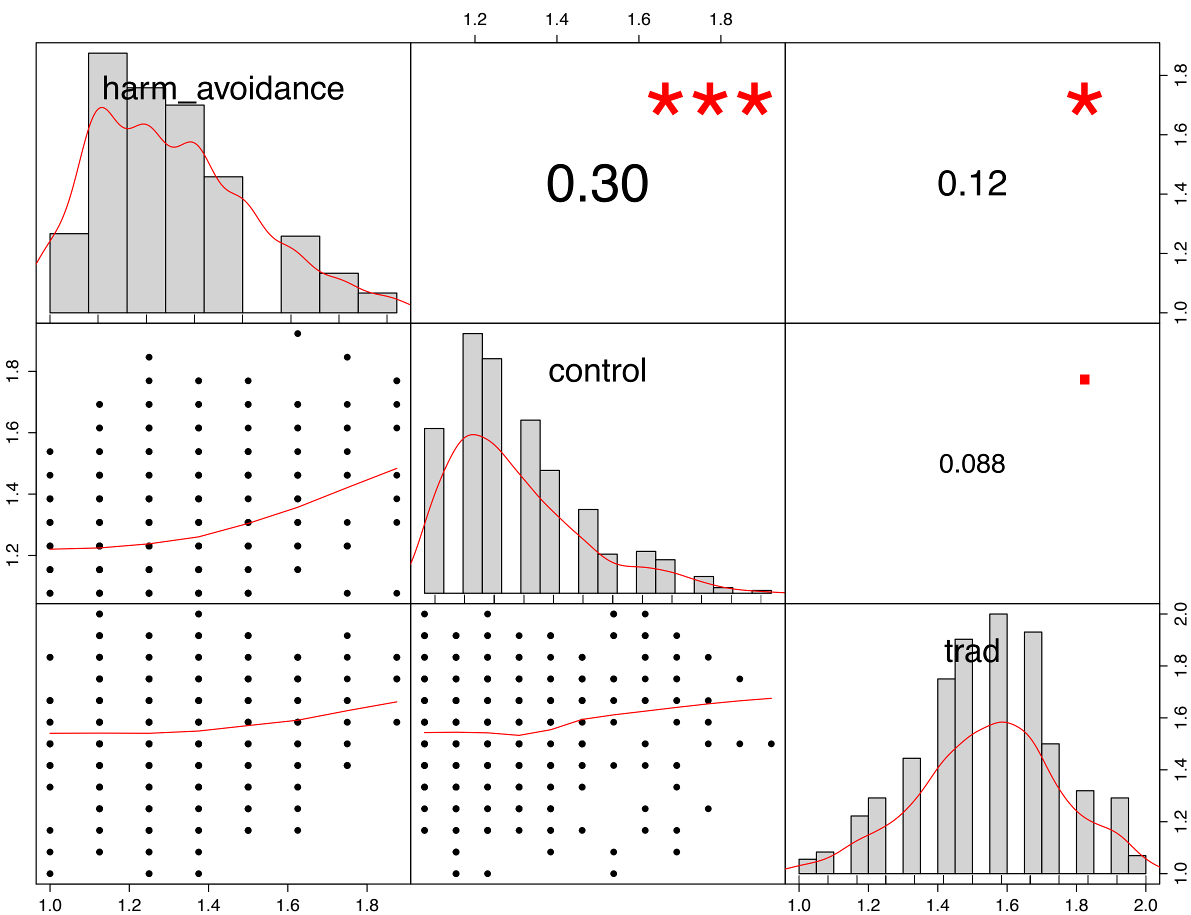


Figure 28.

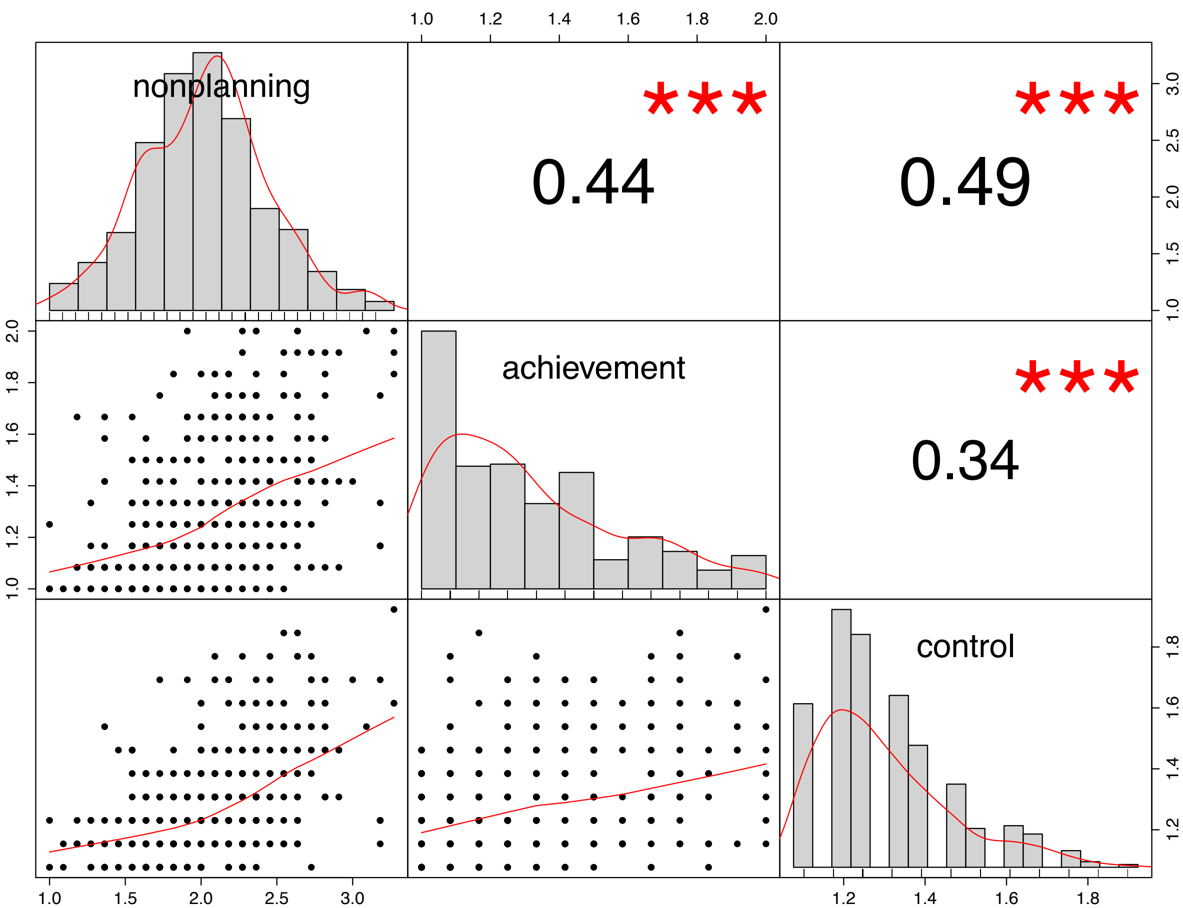

nonplanning
achievement
control
0.44
0.49
0.34
***
***
***
1.0
1.2
1.4
1.6
1.8
2.0
1.0
1.5
2.0
2.5
3.0
1.2
1.4
1.6
1.8

Figure 29.

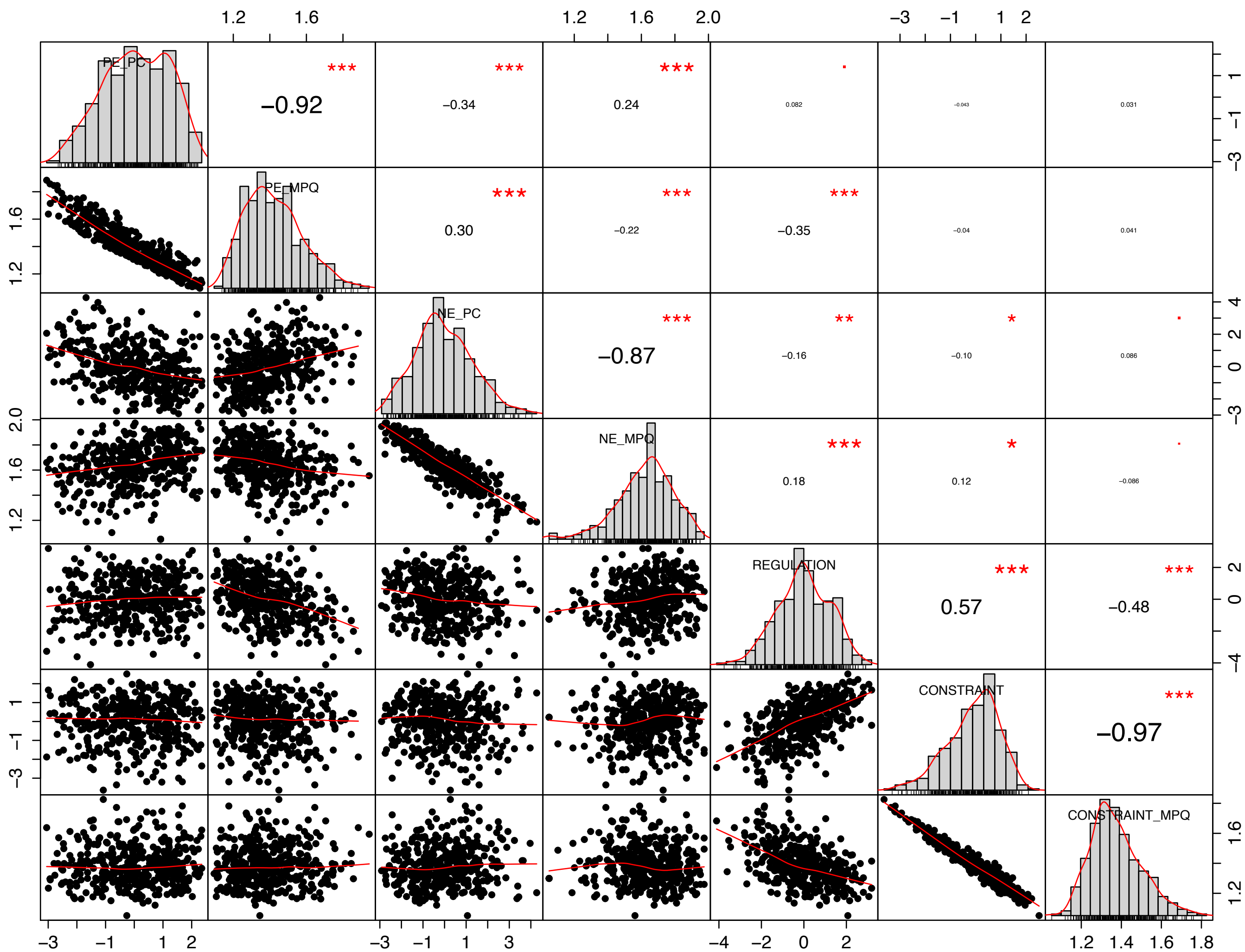

PE_PC
PE_MPQ
NE_PC
NE_MPQ
REGULATION
CONSTRAINT
CONSTRAINT_MPQ
-0.92
-0.34
0.24
0.082
0.30
-0.22
-0.35
-0.87
-0.16
-0.10
0.18
0.12
0.57
-0.48
-0.97

Figure 30.

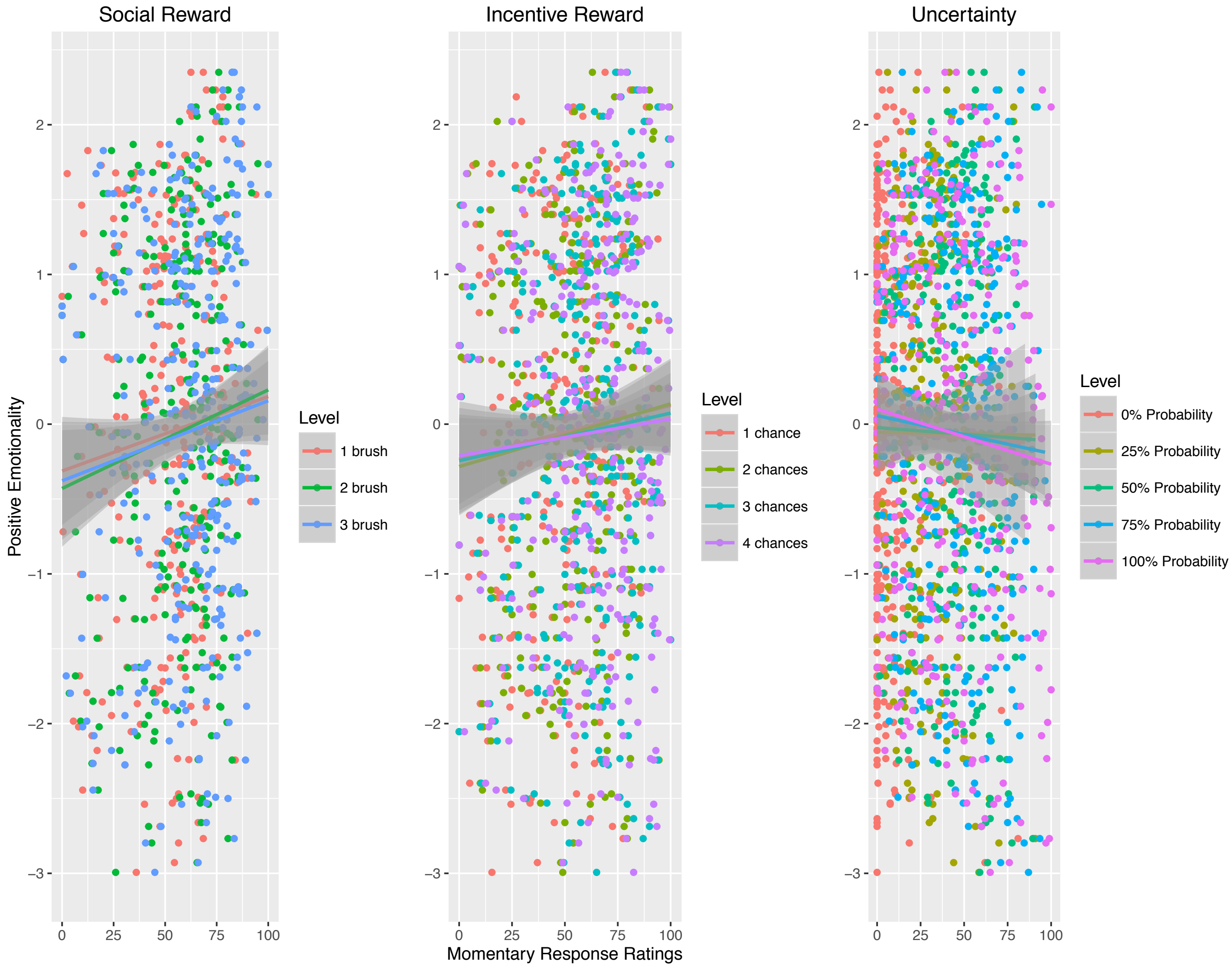

Social Reward
Incentive Reward
Uncertainty
Positive Emotionality
Momentary Response Ratings
2
1
0
−1
−2
−3
0
25
50
75
100
Level
1 brush
2 brush
3 brush
Level
1 chance
2 chances
3 chances
4 chances
Level
0% Probability
25% Probability
50% Probability
75% Probability
100% Probability

Figure 31.

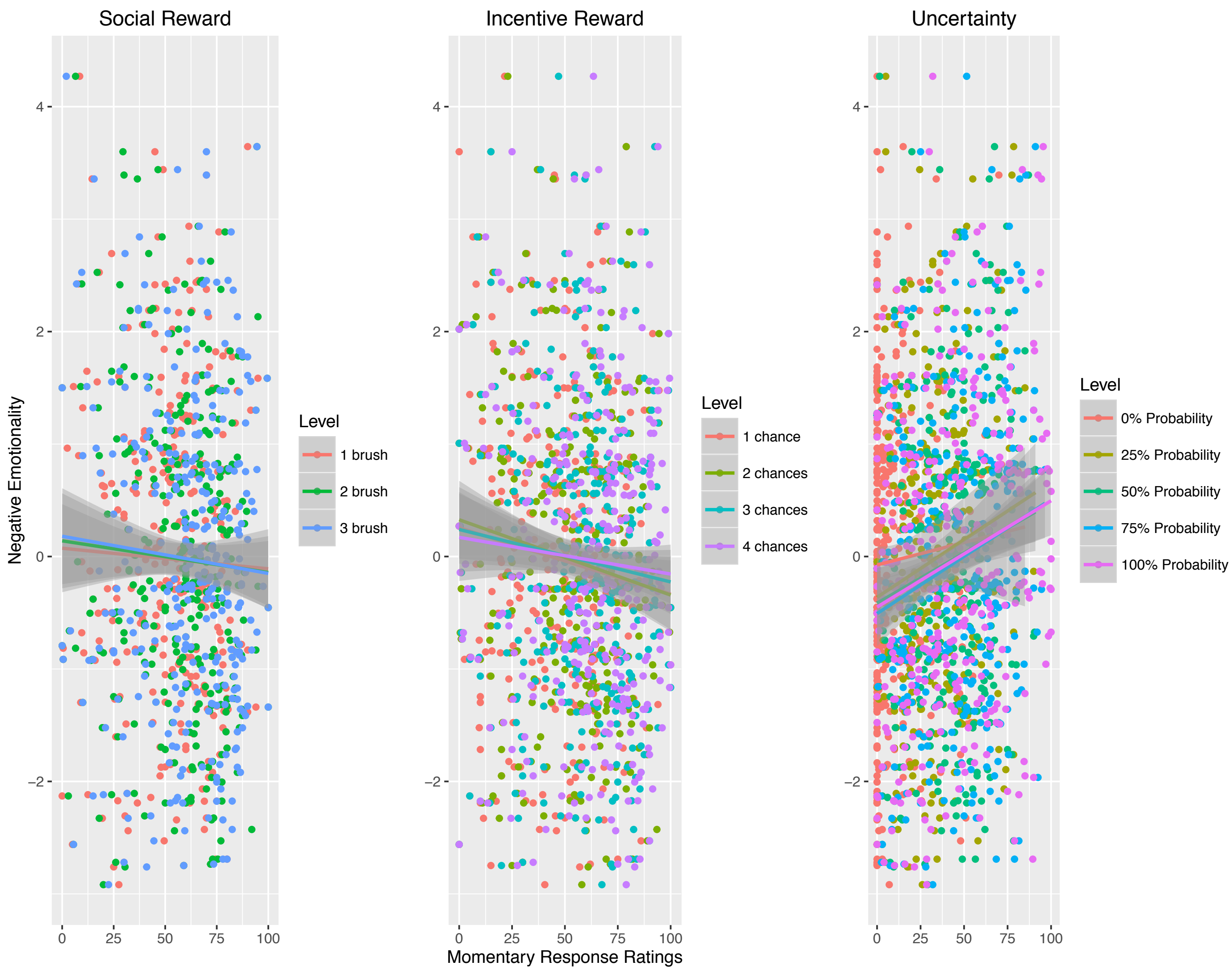

Social Reward
Incentive Reward
Uncertainty
Negative Emotionality
Momentary Response Ratings
Level
1 brush
2 brush
3 brush
Level
1 chance
2 chances
3 chances
4 chances
Level
0% Probability
25% Probability
50% Probability
75% Probability
100% Probability
4
2
0
−2
0
25
50
75
100

Figure 32. Traditional Constraint

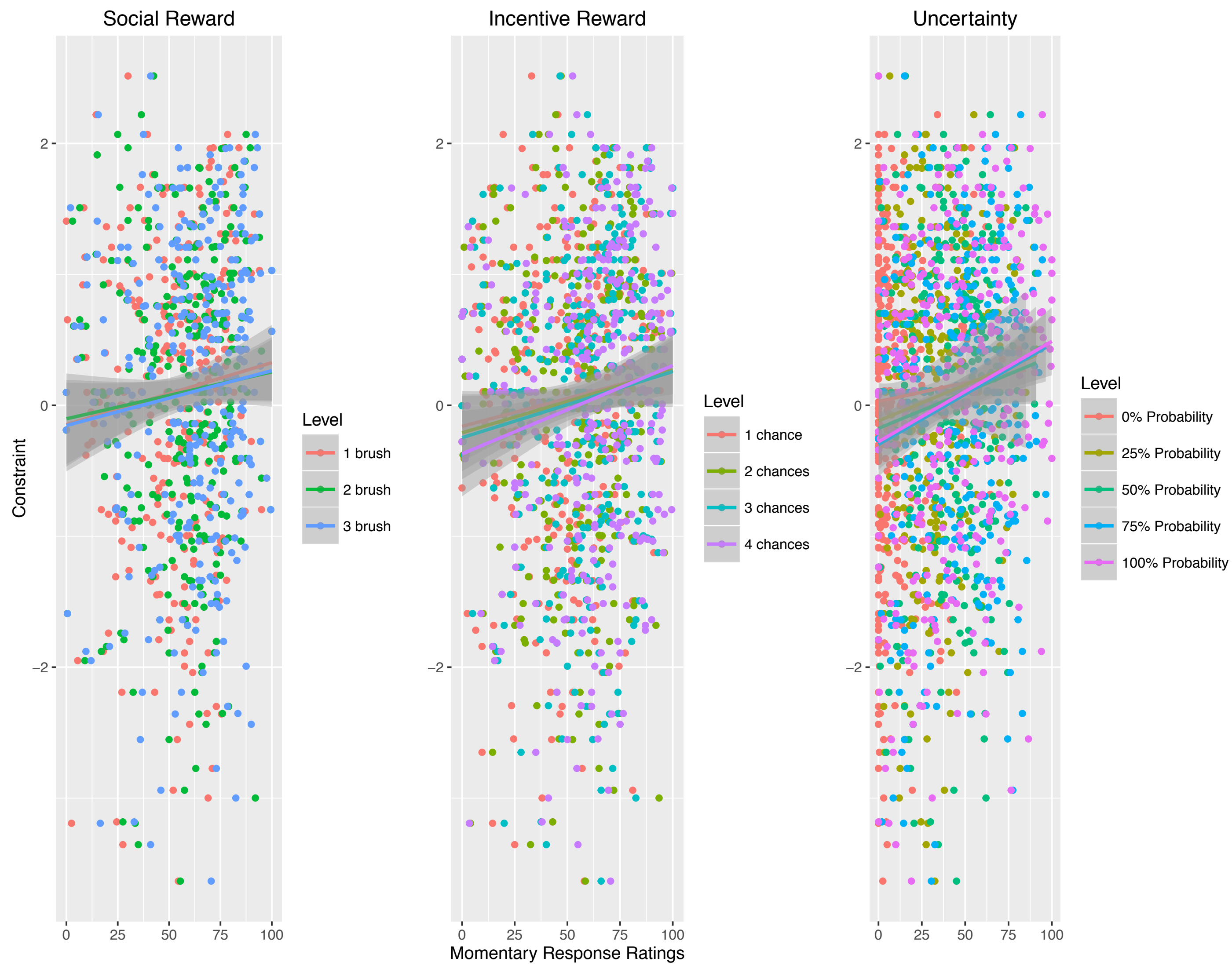


Figure 33. My constraint

Figure 34.

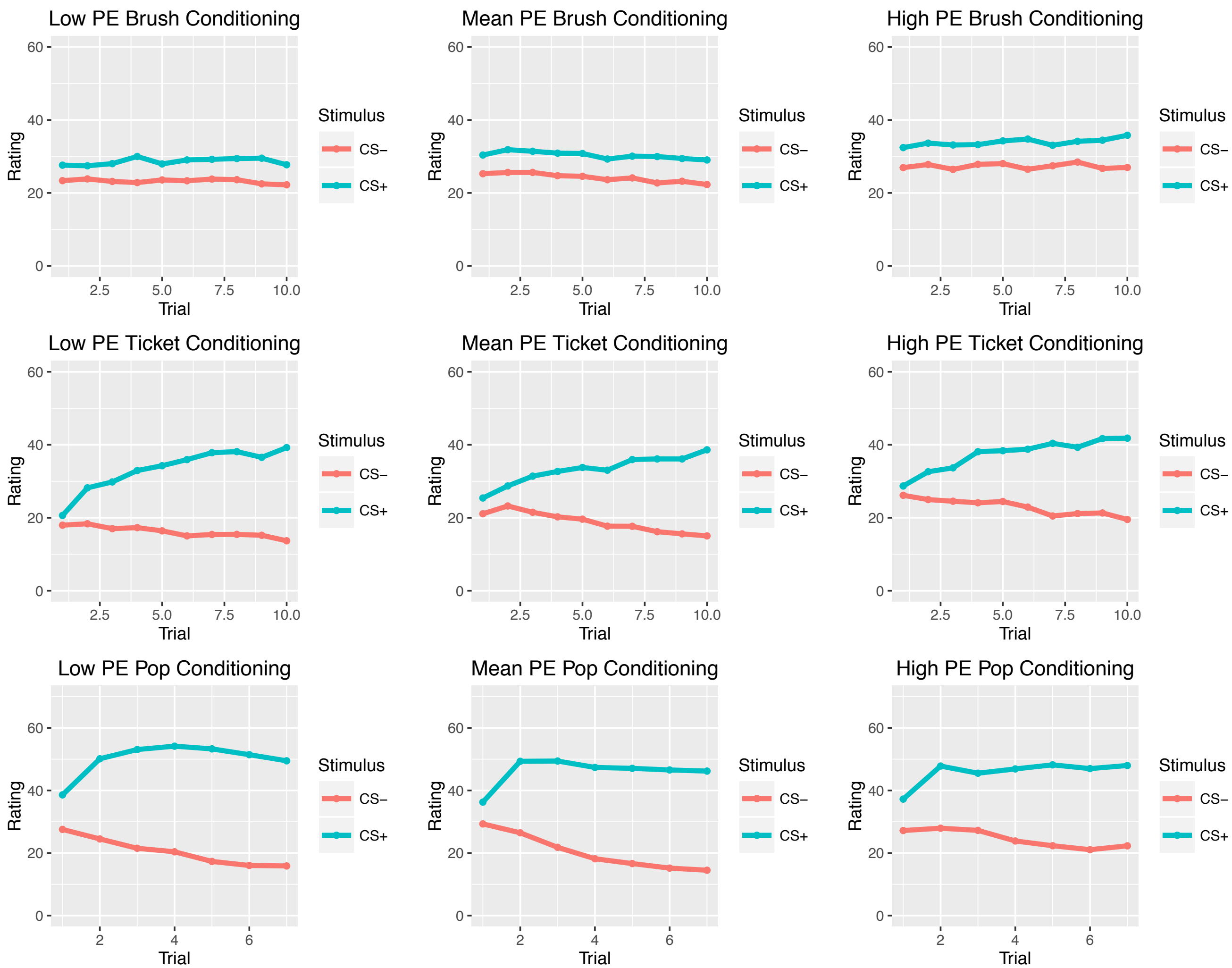

Low PE Brush Conditioning
Mean PE Brush Conditioning
High PE Brush Conditioning
Low PE Ticket Conditioning
Mean PE Ticket Conditioning
High PE Ticket Conditioning
Low PE Pop Conditioning
Mean PE Pop Conditioning
High PE Pop Conditioning
Rating
Trial
Stimulus
CS–
CS+

Figure 35.

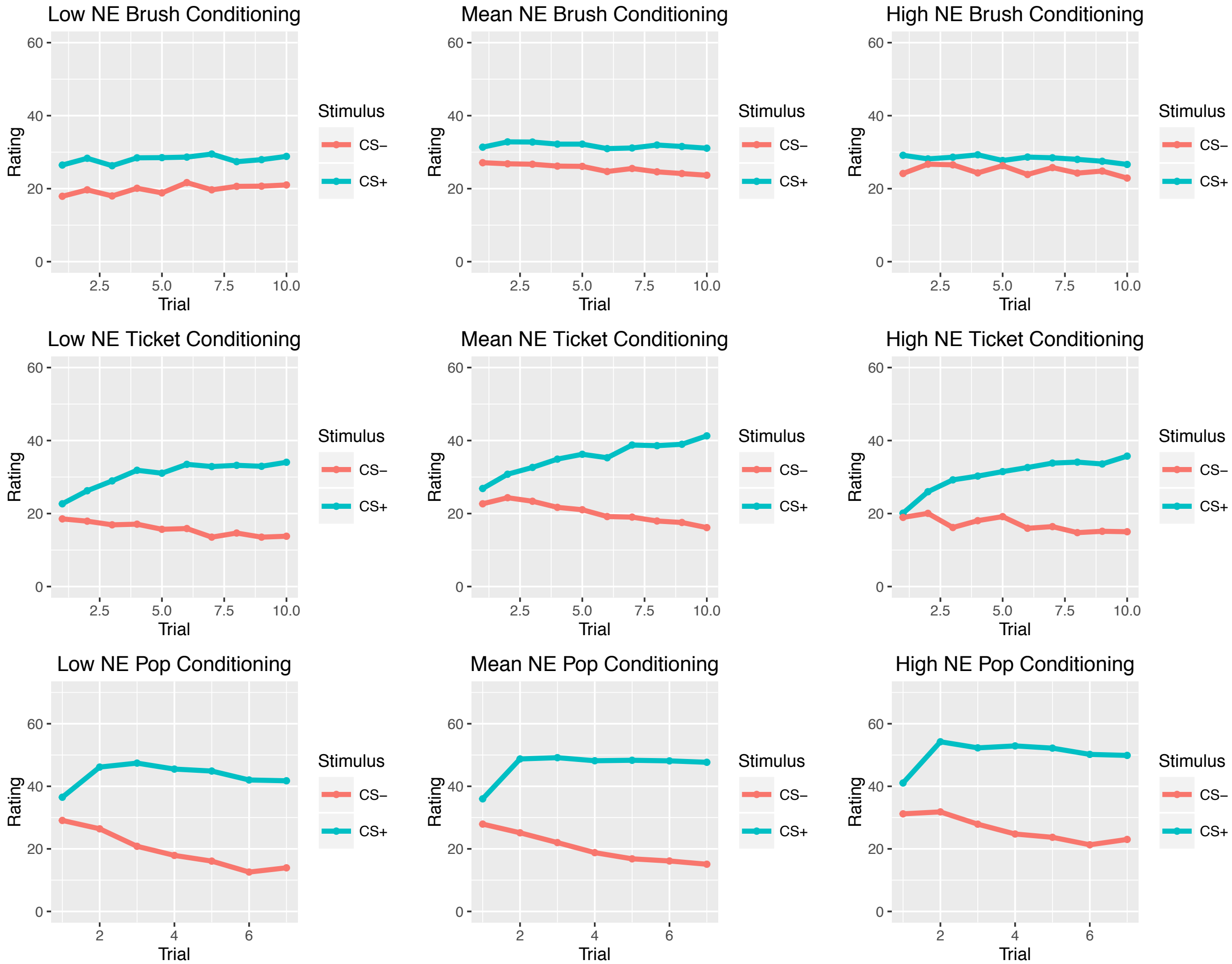

Low NE Brush Conditioning
Mean NE Brush Conditioning
High NE Brush Conditioning
Low NE Ticket Conditioning
Mean NE Ticket Conditioning
High NE Ticket Conditioning
Low NE Pop Conditioning
Mean NE Pop Conditioning
High NE Pop Conditioning
Rating
Trial
Stimulus
CS–
CS+

Figure 36. Traditional

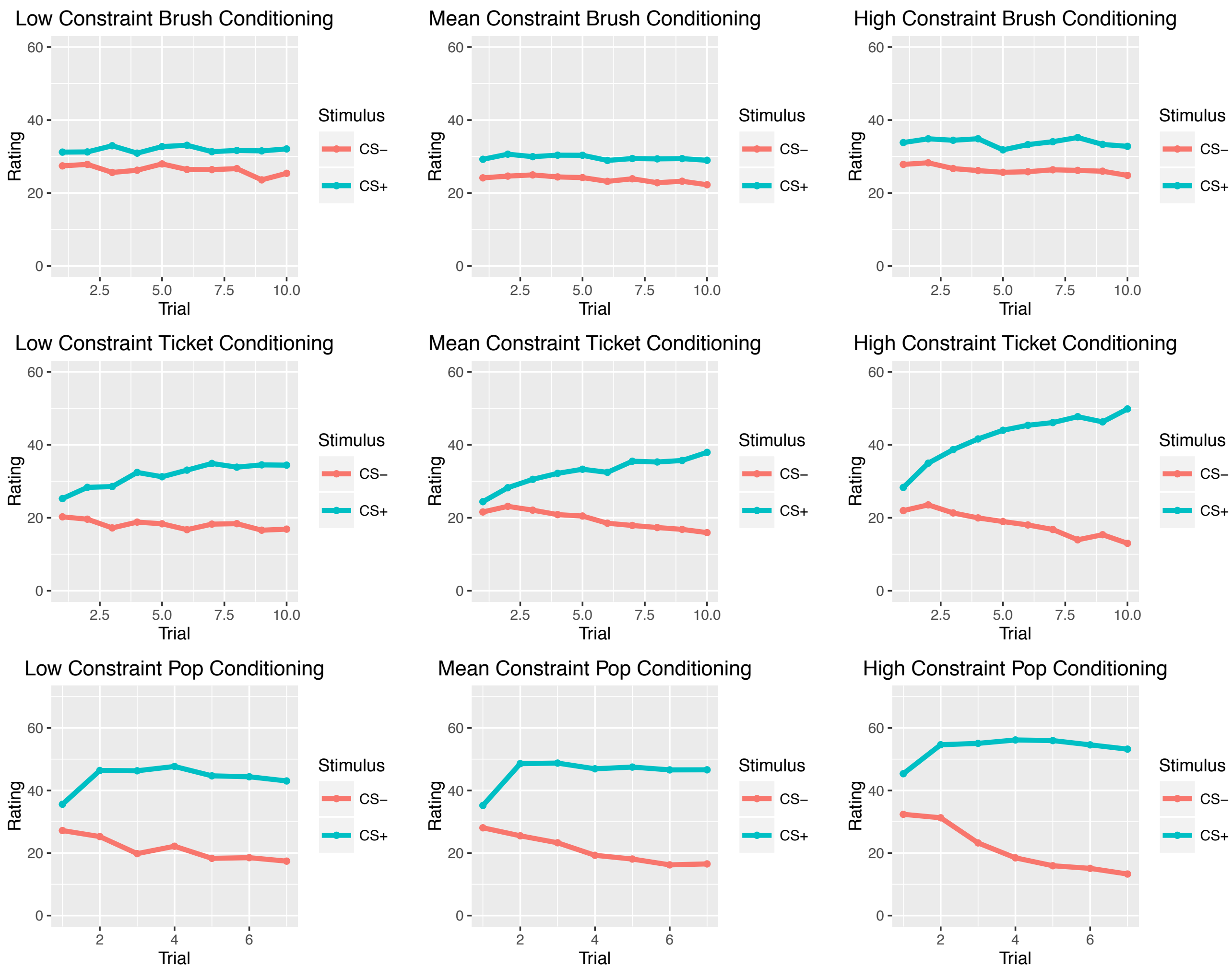


Figure 37. My constraint

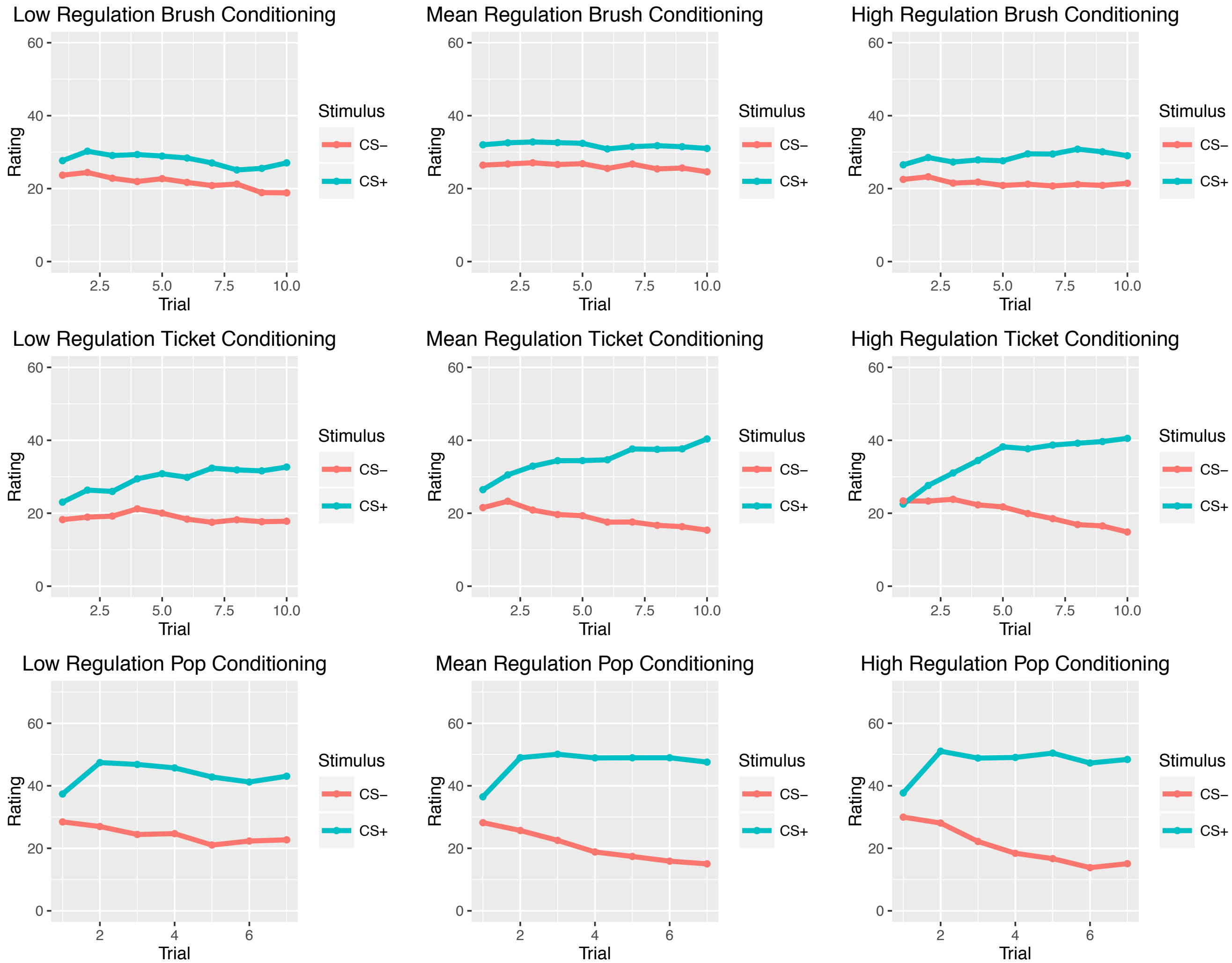
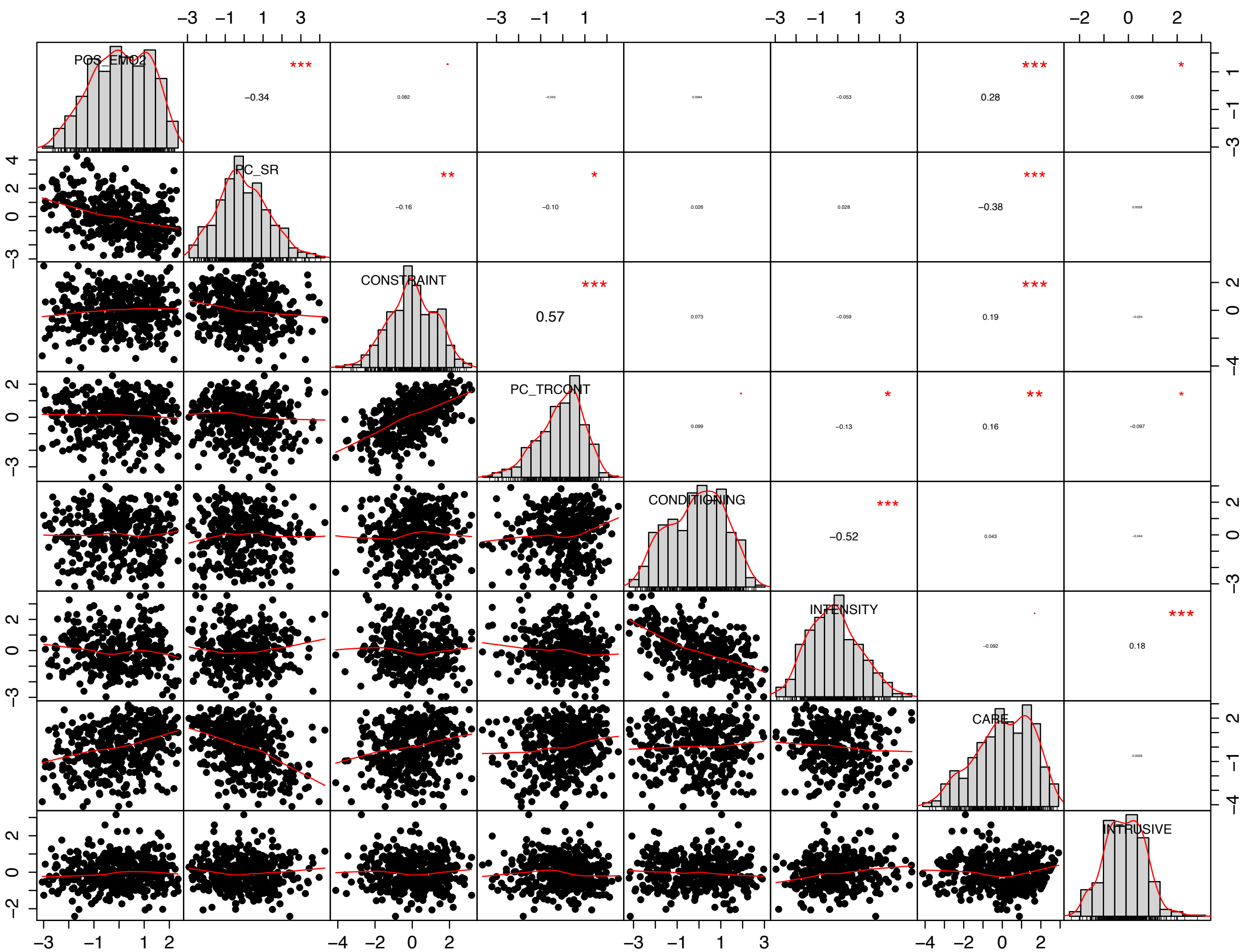


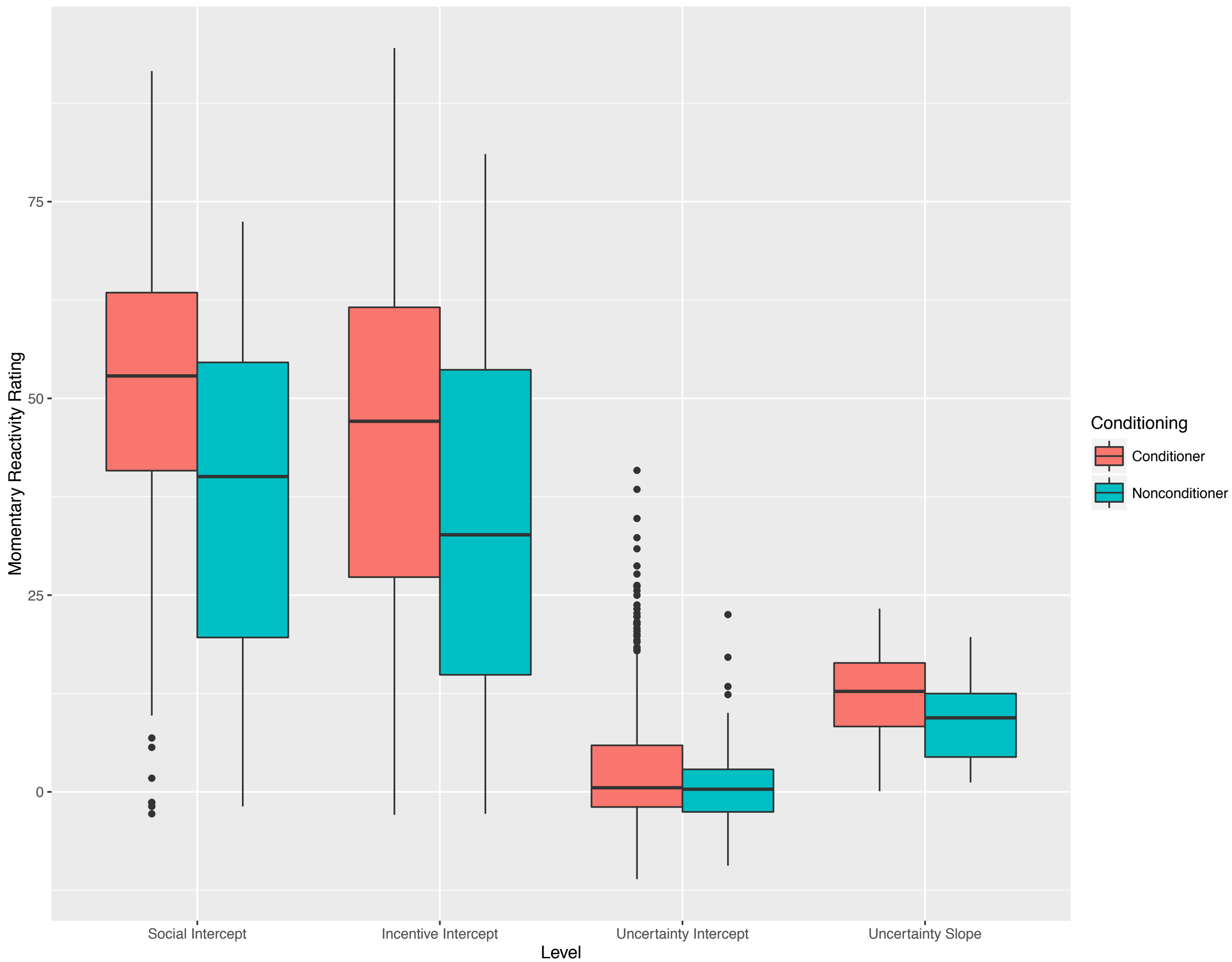
Figure 38.


POS_EMO2
PC_SR
CONSTRAINT
PC_TRCONT
CONDITIONING
INTENSITY
CARE
INTRUSIVE
-0.34
0.28
-0.38
0.57
0.19
0.16
-0.52
0.18

Conditioners Versus Nonconditioners. Before running final models to determine statistical significance of these relationships, further investigation into experimental outcomes, environmental history, and personality traits was carried out for conditioners versus non-conditioners. In traditional studies of associative conditioning, non-conditioners are often completely omitted from analyses. Here, it is preferable to keep these individuals as they likely reflect some end of the targeted sensitivity spectrum, at least in terms of emotional learning, that is of interest.

The average momentary reactivity ratings for conditioners and nonconditioners across tasks is displayed in Figure 39. As would be expected based on the relationships explored above between momentary reactivity and conditioning for each system, conditioners display higher momentary reactivity across tasks relative to nonconditioners. Figure 40 shows the average levels of each higher-order personality trait for conditioners and nonconditioners. There are minimal differences between conditioners and nonconditioners in positive emotionality. Nonconditioners have slightly higher levels of negative emotionality and lower levels of constraint and regulation relative to conditioners. The relation between lower constraint/regulation and nonconditioning lends some support to the notion that the degree of emotional learning might capture a regulatory strategy of ‘pause and check’ in encounters with the environment. Figure 41 displays early environmental components for conditioners and nonconditioners. Conditioners report slightly higher quality early environment and slightly higher parent overprotection relative to nonconditioners. In final models, conditioning propensity across emotional tasks is not modeled categorically. The principle component created from conditioning scores across the three tasks is used as this captures full variation.

Figure 39.



Momentary Reactivity Rating
75
50
25
0
Social Intercept
Incentive Intercept
Uncertainty Intercept
Uncertainty Slope
Level
Conditioning
Conditioner
Nonconditioner

Figure 40.

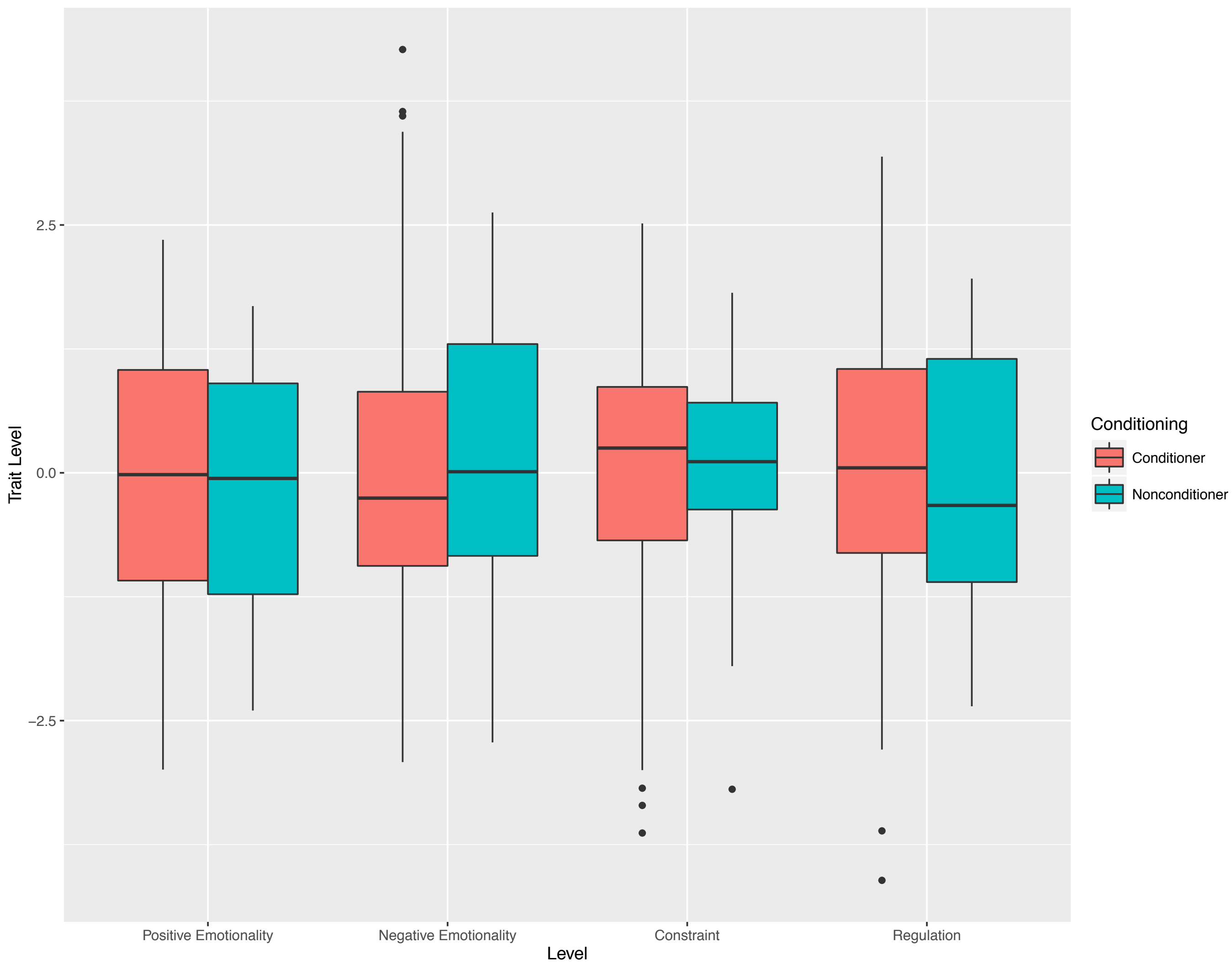
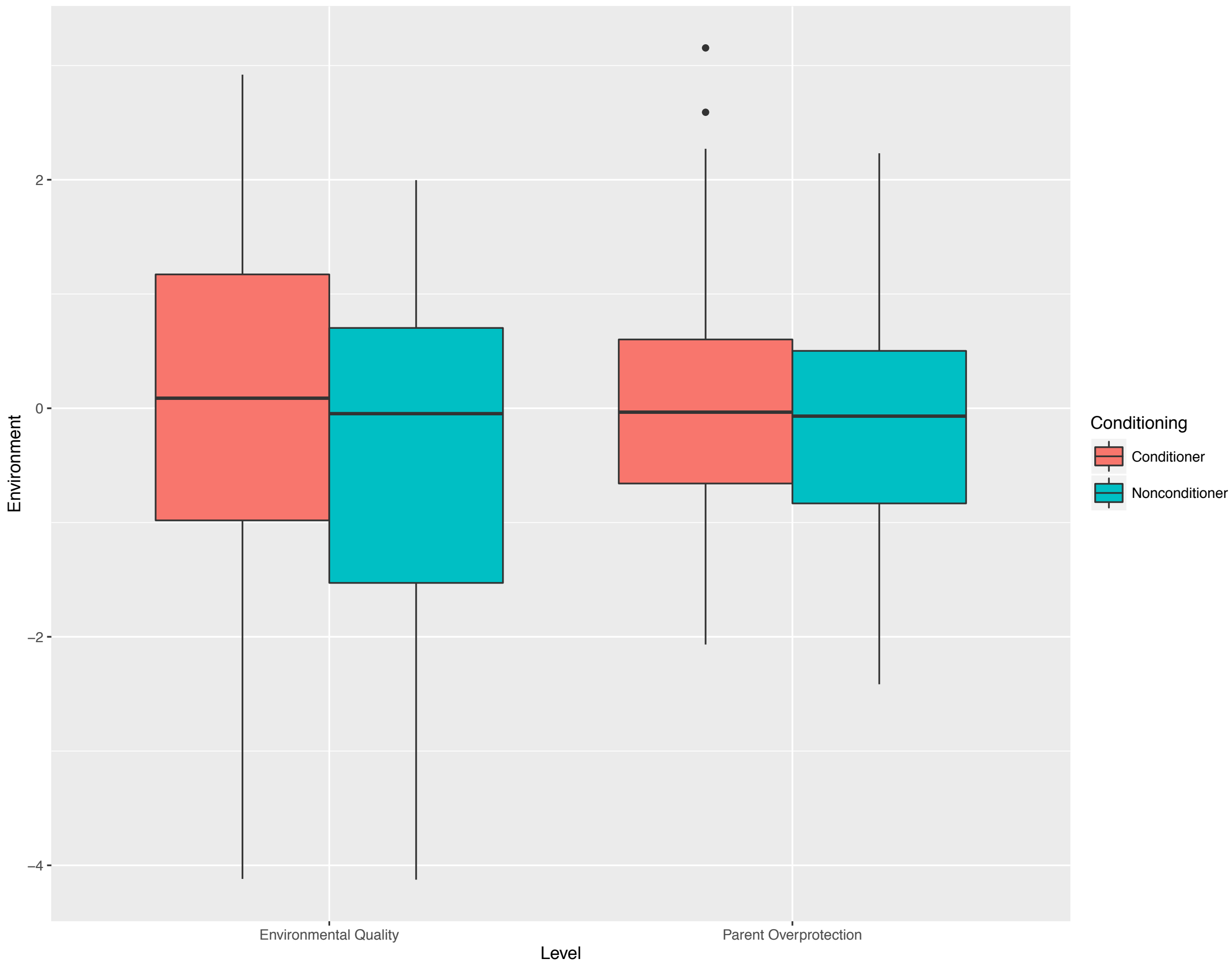

2.5
0.0
−2.5
Trait Level
Positive Emotionality
Negative Emotionality
Constraint
Regulation
Level
Conditioning
Conditioner
Nonconditioner

Figure 41.



2
0
−2
−4
Environment
Environmental Quality
Parent Overprotection
Level
Conditioning
Conditioner
Nonconditioner

Final Models

Final structural equation models were carried out to test the statistical significance of the hypothesized relations among experimental sensitivity scores, early environments, and personality traits. These models are displayed in Figures 42-44. Each of the four models corresponds with a component of the proposed model, including sensitivity to social and incentive rewards and positive emotionality (model 1), sensitivity to uncertainty/stress and negative emotionality (model 2), and sensitivity across emotional systems and constraint/regulation (models 3 and 4). In all models the two environmental PCs (Env1 = environmental quality and Env2 = overprotection) are modeled to affect threshold/momentary reactivity, conditioning/emotional learning, and the behavioral outcome. Threshold indices have effects on respective conditioning indices, and both threshold and conditioning indices have paths to the behavioral outcome. Finally, the sensitivity predictors in the constraint models are the general sensitivity PCs created for threshold and for conditioning collapsed across emotional systems.

These models allow for the hypotheses described above to be tested. If enriching environments promote responsiveness of the incentive reward and social bonding systems, and higher regulatory capacity over emotional responses, then pathways from environmental factors (especially Env1 which is a dimension spanning adverse to enriched family life) to indices of social and incentive reward sensitivity should be significant. Likewise, if stressful environments upregulate stress reactivity, then pathways are expected from environmental factors to gauges of threshold and emotional learning to stress.

Furthermore, if these biological systems, in part, shape broader behavioral trajectories, they should relate to corresponding personality traits. Specifically, paths are expected from reward sensitivity gauges to sociality and impulsive approach, from stress sensitivity gauges to stress reactivity, and from general sensitivity indicators to behavioral constraint. Finally, environmental factors, in addition to their effects on biological sensitivity, are expected to relate to corresponding behavioral outcomes as well. The results of all four models are described below, and displayed in Tables 4-7.

Figure 42.

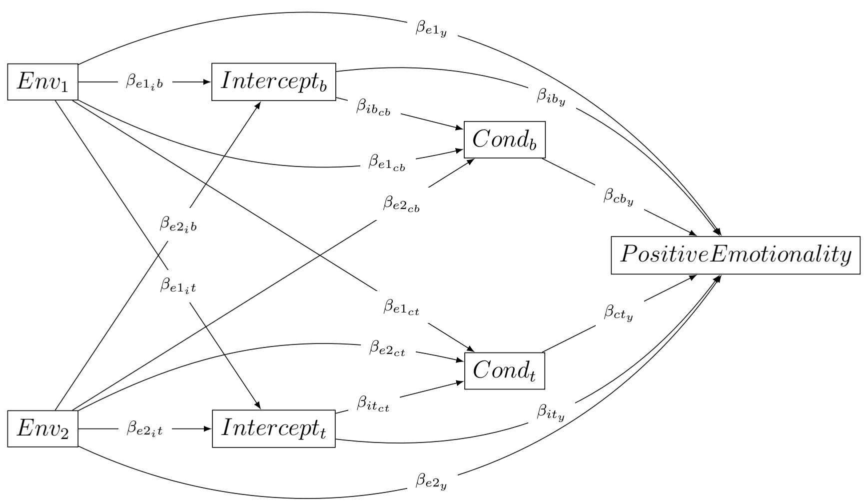


Figure 43.

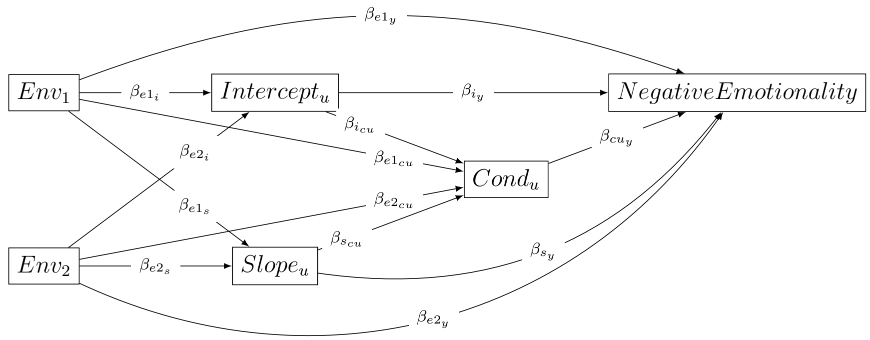
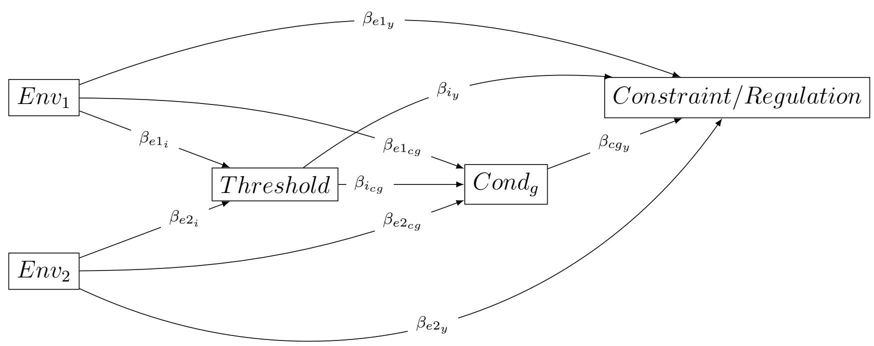


Figure 44.



Note for Figures 42-44. Env1 = environmental quality from adverse to enriched; Env2 = parent overprotection; b = brush (social reward); t = ticket (incentive reward); u = uncertainty (stress); g = general (combined across specific emotional sensitivities).

Table 4. Final Model Results for Social and Incentive Reward and Positive Emotionality

parameter	est	se	pvalue	ci.lower	ci.upper
βiby	0.05	0.06	0.36	-0.06	0.17
βity	0.06	0.06	0.32	-0.06	0.17
βcby	0.10	0.07	0.12	-0.03	0.23
βcty	-0.11	0.06	0.09	-0.24	0.02
βe1y	**0.25**	**0.05**	**0.00**	**0.15**	**0.35**
βe2y	**0.12**	**0.05**	**0.02**	**0.02**	**0.23**
βsex	-0.07	0.05	0.16	-0.17	0.03
βage	-0.09	0.05	0.07	-0.20	0.01
βses	0.08	0.05	0.11	-0.02	0.19
βibcb	**0.44**	**0.05**	**0.00**	**0.34**	**0.53**
βe1cb	0.04	0.05	0.38	-0.05	0.14
βe2cb	-0.03	0.05	0.58	-0.12	0.07
βitct	**0.41**	**0.05**	**0.00**	**0.31**	**0.50**
βe1ct	0.03	0.05	0.59	-0.07	0.13
βe2ct	0.06	0.05	0.20	-0.03	0.16
βe1ib	**0.12**	**0.05**	**0.02**	**0.02**	**0.23**
βe2ib	**-0.16**	**0.05**	**0.00**	**-0.26**	**-0.06**
βe1it	0.04	0.05	0.49	-0.07	0.14
βe2it	**-0.22**	**0.05**	**0.00**	**-0.32**	**-0.12**

Note. Chi-square = 31.84 (df = 12; p = 0.00); Root mean-square error of approximate = 0.07.

Table 5. Final Model Results for Uncertainty and Negative Emotionality

parameter	est	se	pvalue	ci.lower	ci.upper
βiy	-0.05	0.05	0.31	-0.15	0.05
βsy	**0.13**	**0.06**	**0.02**	**0.02**	**0.24**
βcuy	0.02	0.06	0.67	-0.09	0.14
βe1y	**-0.37**	**0.05**	**0.00**	**-0.47**	**-0.27**
βe2y	0.03	0.05	0.52	-0.06	0.12
βsex	0.08	0.05	0.07	-0.01	0.18
βage	**-0.11**	**0.05**	**0.02**	**-0.20**	**-0.01**
βses	0.04	0.05	0.43	-0.06	0.13
βicu	**0.19**	**0.04**	**0.00**	**0.10**	**0.27**
βscu	**0.56**	**0.04**	**0.00**	**0.48**	**0.64**
βe1cu	-0.02	0.04	0.69	-0.10	0.07
βe2cu	0.03	0.04	0.42	-0.05	0.11
βe1i	**-0.17**	**0.05**	**0.00**	**-0.27**	**-0.08**
βe2i	**0.10**	**0.05**	**0.04**	**0.01**	**0.19**
βe1s	0.07	0.05	0.17	-0.03	0.18
βe2s	-0.06	0.05	0.26	-0.15	0.04

Note. Chi-square = 33.85 (df = 10; p = 0.00); Root mean-square error of approximate = 0.08.

Table 6. Final Model Results for General Reactivity and Constraint (Traditional)

parameter	est	se	pvalue	ci.lower	ci.upper
βiy	-0.01	0.06	0.88	-0.13	0.11
βcgy	0.11	0.06	0.06	-0.01	0.23
βe1y	**0.11**	**0.05**	**0.04**	**0.01**	**0.22**
βe2y	-0.09	0.05	0.08	-0.19	0.01
βsex	**0.17**	**0.05**	**0.00**	**0.06**	**0.27**
βage	0.01	0.05	0.80	-0.09	0.11
βses	-0.02	0.05	0.69	-0.12	0.08
βicg	**-0.52**	**0.05**	**0.00**	**-0.61**	**-0.42**
βe1cg	-0.01	0.05	0.80	-0.11	0.08
βe2cg	0.04	0.05	0.35	-0.05	0.14
βe1i	-0.10	0.06	0.07	-0.21	0.01
βe2i	**0.18**	**0.05**	**0.00**	**0.07**	**0.28**

Note. Chi-square = 4.21 (df = 6; p = 0.65); Root mean-square error of approximate = 0.00.

Table 7. Final Model Results for General Reactivity and Constraint (Regulation)

parameter	est	se	pvalue	ci.lower	ci.upper
βiy	0.01	0.06	0.91	-0.12	0.13
βcgy	0.07	0.06	0.22	-0.04	0.19
βe1y	**0.18**	**0.06**	**0.00**	**0.07**	**0.29**
βe2y	-0.05	0.05	0.36	-0.15	0.06
βsex	0.10	0.05	0.07	-0.01	0.20
βage	0.01	0.05	0.81	-0.09	0.11
βses	0.09	0.05	0.08	-0.01	0.20
βicg	**-0.52**	**0.05**	**0.00**	**-0.61**	**-0.42**
βe1cg	-0.01	0.05	0.80	-0.11	0.08
βe2cg	0.04	0.05	0.35	-0.05	0.14
βe1i	-0.10	0.06	0.07	-0.21	0.01
βe2i	**0.18**	**0.05**	**0.00**	**0.07**	**0.28**

Note. Chi-square = 31.84 (df = 12; p = 0.00); Root mean-square error of approximate = 0.07.

Reward and Positive Emotionality. Both environmental components (quality and overprotection) relate to momentary reactivity to social reward, such that higher quality environments predict greater reactivity to social reward, and overprotection predicts reduced reactivity to social reward. Overprotection additionally significantly predicts momentary reactivity to incentive reward (negative association), suggesting that overprotection leads to reduced responsiveness to incentives. Conditioning to both social and incentive reward relates to momentary reactivity to social and incentive reward, respectively. There were no effects of the environment on conditioning.

Environmental quality positively relates to positive emotionality, and there are no effects of overprotection, momentary reactivity or conditioning (social or incentive reward) on positive emotionality. Thus, a tendency to be socially engaged and to experience positive emotions is not related to reward sensitivity, but is predicted by environments high in nurturance and safety and low in stress.

Uncertainty and Negative Emotionality. In the uncertainty/negative emotionality model, both the intercept (baseline anxiety) and slope (rate of increase in anxiety with increasing uncertainty) are included as gauges of momentary reactivity/threshold. Environmental quality has a positive association, and overprotection a negative association with uncertainty intercept. There are no effects of environment on uncertainty slope. Both intercept and slope significantly predict conditioning.

Environmental quality has a negative effect on negative emotionality, and slope has a positive effect on negative emotionality. Nurturing and safe environments relate to reduced negative emotionality, and stressful, abusive, and unsafe environments relate to higher negative emotionality. Additionally, the rate at which anxiety is raised in response to increasing uncertainty relates to heightened negative emotionality.

General Reactivity and Constraint/Regulation. Overprotection, but not environmental quality, predicts general reactivity threshold, such that overprotection has a positive effect on both traditional constraint and regulation. General momentary reactivity has a positive effect on general conditioning. Thus, when momentary reactivity and conditioning are collapsed across specific emotional systems, a measure of general reactivity in the moment to emotional cues relates to enhanced reflection and emotional learning. It is noteworthy that the highest loadings on the general momentary reactivity principle component are from social and incentive rewards, suggesting that this principle component is weighted more towards reactivity to rewards than stressors.

Constraint and regulation, describing highly planful and regulated behavior was not predicted by general sensitivity indices, including momentary reactivity and conditioning. There is a significant effect of environmental quality on constraint, such that greater care and safety, and reduced stress relate to higher levels of regulated behavior.

Discussion

In this investigation, a large sample of young adults were characterized in terms emotional sensitivities in accordance with a comprehensive neurobiological model of sensitivity to the environment. The environmental precursors of these quantified emotional sensitivities, and potential relations with current behavioral tendencies were also assessed. The main findings suggest that the biological sensitivity of these emotional systems, as well as associated behavioral tendencies, are related to the quality of early environments. Enrichment fosters sensitivity to rewards, as well as positive emotionality and regulated, goal-oriented behavior. Adversity appears to upregulate sensitivity to stressors, in addition to promoting impulsive, unconstrained behavior.

The first aim of this investigation was to quantify sensitivity to the environment with experimental procedures targeting the responsiveness of specific emotional systems. These procedures enabled the measurement of both momentary emotional reactivity and emotional learning. These two components are critical because the essence of being sensitive is being malleable to experience. Developmental change to experiences requires both an initial response, or reading of the environmental cue by the individual, and for that experience to become engrained in biology. Here initial responses were captured via ratings of subjective feelings to primary emotional cues, including rewarding soft touch, incentives, and uncertainty. The magnitude of these ratings represent the strength of the social bonding, incentive motivation, and anxiety emotional systems, respectively. Subsequently, the degree that the experience becomes engrained in biology was represented by the strength of affective conditioning to the neutral environmental cues associated with the primary stimulus. The degree that the neutral context became associated with the emotional feelings elicited by the stimulus reflects the degree that the emotional experience was processed in depth and engrained in emotional memory.

According to the model, the strength of the three targeted emotional systems influences how deeply emotional experiences are processed and engrained in neural circuitries, linking variation in each emotional system to variation in sensitivity to the environment. The findings from this study support this prediction: momentary responsiveness to soft touch, incentive reward, and uncertainty each strongly associated with emotional learning, linking the reactivity of each of these emotional systems to depth of processing of the corresponding cue and its context. Overall, these results suggest that the activation of these three emotional-motivational systems, identified by the environmental sensitivity literature, provide the means of adapting to contexts, and that variation in the strength of each system corresponds with variation in adaptation to those contexts.

Another important component of the model is the construct of neural constraint, which includes neural variables (e.g., NE) with general, constraining effects upon the specific emotional systems. In an effort to capture variation in neural constraint using the experimental indices of sensitivity to rewards and stressors, scores of momentary reactivity, and of conditioning strength were combined across systems to create measures of general momentary reactivity and conditioning propensity. In exploring individual scores across the three systems visually, general conditioning propensity but not momentary reactivity demonstrates expected trends with behavioral indicators of constraint. Possibly, this general index of conditioning is picking up to some degree on a general gauge of sensitivity, reflecting the tendency to ‘pause and check’ and reflect on experiences. Further comment can be found below on quantifying neural constraint using neural measures.

The second aim of this study was to assess, retrospectively, the early environmental experiences hypothesized to shape emotional sensitivities assessed in the laboratory. The proposed neurobiological framework suggests that early environmental experiences themselves are critical to shaping emotional sensitivities to the environment. The plasticity of developing emotional networks, like any aspect of biological development, is intrinsically linked to the signals in the surrounding environment. Positive experiences are expected to activate and strengthen reward networks, and uncontrollable stressful experiences are expected to do the same for stress reactivity networks. This hypothesis was supported by the current findings. High quality, enriched early environments had positive effects on momentary responsiveness to social reward. Intrusive, overprotective parenting reduced responsive to incentive rewards, suggesting that overbearing parenting can inhibit the approach system. Finally, stressful, unsafe, and abusive early environments positively influenced responsiveness to cues of uncertainty.

Environmental experiences do not relate significantly to conditioning propensity for any emotional system. Rather, momentary responsiveness, likely shaped by the interplay of genetic factors and environmental history, is the only factor here that predicted emotional learning. This finding highlights what exactly is being captured by emotional learning in the current study. Emotional learning is the process though which experiences become registered to affect biology and development long-term. Thus, it is certainly a possibility (and expected based on the model) that emotional learning across developmental history is responsible for the current relationship between retrospective environmental measures and current momentary emotional reactivity. The past environment does not necessarily have any effect on current emotional learning, which is driven directly by the sensitivity of emotional systems.

The third aim was to assess whether emotional sensitivity assessed in the laboratory and early environmental factors predict broader personality dimensions. This aim stems from the notion that the proposed neurobiological model of environment sensitivity can account for findings that particular emotion-related traits serve as markers of sensitivity to environmental experiences. Moreover, following the developmental predictions of the proposed model, it is expected that personality traits reflect both developmental history of early environmental experiences, as well as underlying emotional sensitivities. Consistent with expectations, early experiences relate to broader behavioral patterns. Specifically, enriched environments relate to heightened sociality and behavioral constraint, and stressful environments relate to stress reactivity, and emotional dysregulation/low constraint.

Results are less consistent in terms of connections between experimental measures of emotional sensitivities and personality outcomes. Positive emotionality was not related to momentary responsiveness or conditioning to rewards, and behavioral constraint was not related significantly to general momentary emotional reactivity or conditioning. Negative emotionality was predicted by the rate in which anxiety was increased by heightened uncertainty in the laboratory. In the case of stress reactivity, then, it appears that stress responses in the laboratory context translate to self-reported negative emotionality in daily life. Behaviorally, stress reactivity and negative emotionality appear tightly linked. In contrast, positive emotionality might reflect a more complex mix of processes. For instance, reward sensitivity might only relate to positive emotionality with the addition of regulatory capacity to channel behavior towards achieving rewards and healthy social relationships.

General momentary reactivity and conditioning propensity did not relate to behavioral constraint constructs, including a traditional constraint measure and one more specifically tapping emotion regulation. It could be the case that collapsing across emotional sensitivities is not an adequate means of gauging general sensitivity, whether momentary sensitivity or emotional learning. One assumption of the proposed model is that neural constraint is an over-arching, independent component that acts equally upon emotional sensitivities. Perhaps this part of the model requires modification. It is possible that neural constraint varies in inhibitory strength upon different emotional systems, given that one's history of experiences may have required more frequent 'practice' reflecting upon and regulating emotional responses to particular kinds of experiences. In that case, neural constraint might best be captured by regulated and adaptive behavioral responsiveness to a particular kind of emotional experience (e.g., cognitive abilities used to achieve a reward that is registered as high in value).

Perhaps general sensitivity as captured by conditioning propensity is to some (small) degree a marker of general depth of processing due to underlying constraint process. There is at least a marginal association of nonconditoning with lower emotion regulation. In other words, as would be expected, individuals who do not learn about contexts tend to be more impulsive and dysregulated, and perhaps do not 'pause and check' to reflect on the environment. It will be possible to follow up on this prediction with more direct gauges of neural activity in response to cues and associated contexts, that is not biased by self-report.

Future Directions

There are two critical next steps to follow the current investigation. First is the addition of more direct gauges of neural responsiveness to rewarding and stressful cues. By assessing the responsiveness of emotional and executive control circuitries during affective conditioning on a trial-by-trial basis, as well as during an extinction procedure, it will be possible to determine if those participants identified as nonconditioners by self report are truly not learning the associations between cue and context. Moreover, the quantification of fine grained neural representations, and their adjustment across trials, will provide direct gauges of neural plasticity to experience, and thus a strong test of whether the emotional processes proposed in the model serve as mechanisms of sensitivity to the environment. Finally, it will be possible to test if variation in the connectivity of neural networks (related to 5-HT and NE function) that process salient cues contribute equally to emotional learning of stressors and rewards within the same individual. This analysis will inform whether the proposed model should be updated to accommodate different levels of neural constraint for different emotional systems.

Second, in the near future, the current sample will be genotyped for polymorphisms commonly studied in the environmental sensitivity literature. Genetic predictors can be added to the current analyses to determine if these commonly targeted genetic factors do relate, as proposed by previous theorists, to neural sensitivity to the environment. More importantly, a key prediction outlined in Figure 4 above can be tested, that is, are trajectories of emotional behavior more highly influenced by environmental quality for 'genetically sensitive' individuals? In summary, these extensions of the current study will provide further insight into the interrelationships between genes related to the function of emotional systems, early experiences, and trajectories of emotional behavior.

Conclusions

In the current sensitivity literature, there is quite the emphasis on genes. These genotypes are proposed to determine who benefits from interventions, enriching resources, and sensitive parents, and who suffers the consequences of stress. Researchers are so confident, they suggest using genotype to select the individuals in a population to receive an intervention (e.g., Belsky, 2014). Fortunately, this is a naïve interpretation of the interactions between genotypes and environment that have become so popular in the recent literature.

The relationship between person and an exposed environment is far more complex than single genetic polymorphisms. Regardless of the factors that influence sensitivity at birth, the biological systems that shape how the organism interacts and responds to its surroundings are themselves changing and adapting across development. This means that the construct of environmental sensitivity becomes increasingly complex and specific over developmental time.

Building from the notion that sensitivity is not a static, predetermined entity, in this dissertation I proposed a model for understanding some of the possible neurobiological variables that could account for variation in responsiveness to experiences. A critical prediction of this model is that the emotional experiences that catch the eye, altering behavior, memories and one's future depend on developmental history. The above investigation confirms that emotional sensitivities are indeed related to early experiences within the home environment. Future work on these biological systems must address the critical early years. During this stage of early development, simple environments of safety and support are likely critical to setting beneficial trajectories of prosocial and regulated behavior across the lifespan.

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APPENDIX

Analysis of Emotional-Motivational Content in Environmental Reactivity Studies

Article	Neurotransmitter System	Environment by Category	Emotional System	Outcome
		Childhood deprivation		
Bakermans et al. (2012)	5-HTTLPR	Institutional care	Uncertainty/stress	Disorganized attachment
Kumsta et al. (2010)	5-HTTLPR	Early institutional deprivation	Uncertainty/stress	Adolescent emotional problems
		Childhood family adversity		
Eley et al. (2004)	5-HTTLPR	Family environmental risk	Uncertainty/stress	Depression symptoms
Nilsson et al. (2005)	5-HTTLPR	Family function	Uncertainty/stress	Adolescent alcohol consumption
Paaver et al. (2008)	5-HTTLPR	Family relations	Uncertainty/stress	Impulsivity in girls
Retz et al. (2008)	5-HTTLPR	Childhood adverse environment	Uncertainty/stress	ADHD
Stein et al. (2008)	5-HTTLPR	Childhood emotional abuse	Uncertainty/stress	Anxiety sensitivity
Taylor et al. (2006)	5-HTTLPR	Early family risk, stressful life events	Uncertainty/stress	Depression symptoms
Cicchetti et al. (2011)	5-HTTLPR, CRHR1	Maltreatment	Uncertainty/stress	Internalizing
Berman & Noble (1997)	DRD2	Family stress	Uncertainty/stress	Visuospatial ability, P300 amplitude
Caspi et al. (2002)	MAOA	Childhood maltreatment	Uncertainty/stress	Antisocial behavior
Ducci et al. (2008)	MAOA	Childhood sexual abuse	Uncertainty/stress	Antisocial personality
Foley et al. (2004)	MAOA	Childhood adversity	Uncertainty/stress	Conduct disorder
Frazzetto et al. (2007)	MAOA	Childhood traumatic life events	Uncertainty/stress	Physical aggression
Kim-Cohen et al. (2006)	MAOA	Physical abuse	Uncertainty/stress	Metal health problems, ADHD
Nilsson et al. (2006)	MAOA	Maltreatment and living conditions	Uncertainty/stress	Criminal behaviors
Widom & Brzustowicz (2006)	MAOA	Childhood abuse/neglect	Uncertainty/stress	Antisocial behavior
Keltikangas-Järvinen et al. (2007)	THP1	Hostile child environment	Uncertainty/stress	Harm avoidance
		Brief and extended stress		
Benjet et al. (2010)	5-HTTLPR	Relational peer victimization	Uncertainty/stress	Depressive symptoms
Brummett et al. (2008)	5-HTTLPR	Caregiver of Alzheimer patient	Uncertainty/stress	Depression symptoms

Caspi et al.(2003)	5-HTTLPR	Stressful life events	Uncertainty/stress	Depression symptoms, suicide ideation
Gunthert et al. (2007)	5-HTTLPR	Daily event stress	Uncertainty/stress	Evening anxiety
Manuck et al. (2004)	5-HTTLPR	SES	Uncertainty/stress; incentive reward	CNS serotonergic responsivity
Mueller et al. (2011)	5-HTTLPR	Stressful life events	Uncertainty/stress	Cortisol stress response in Trier Social Stress Test
Nobile et al. (2007)	5-HTTLPR	SES	Uncertainty/stress; incentive reward	Externalizing
Sadeh et al. (2010)	5-HTTLPR	SES	Uncertainty/stress; incentive reward	Youth psychopathic traits
Sugden et al. (2010)	5-HTTLPR	Bullying victimization	Uncertainty/stress	Child emotional problems
Wilhelm et al. (2006)	5-HTTLPR	Stressful life events	Uncertainty/stress	Major depression
Zalsman et al. (2006)	5-HTTLPR	Stressful life events	Uncertainty/stress	Depression symptoms
Waldman (2007)	DRD2	Mother's marital status	Uncertainty/stress	ADHD
Elovainio et al. (2007)	DRD2	Stressful life events	Uncertainty/stress	Depression symptoms
Belsky et al. (2009)	DRD2, DRD4, COMT	Parental divorce	Uncertainty/stress	Adult relationship stability
van IJzendoorn et al. (2008)	DRD4, COMT	Daily hassles	Uncertainty/stress	Maternal sensitivity
Jokela et al. (2007a)	HTR2A	Rural/urban residency	Uncertainty/stress; incentive reward	Depression symptoms
Jokela et al. (2007b)	HTR2A	Parental SES	Uncertainty/stress; incentive reward	Harm avoidance
		Negative manipulation		
Verona et al., (2006)	5HTTLPR	Physical stressor	Uncertainty/stress	Aggression
Gallardo et al. (2013)	MAOA	Social exclusion	Social reward/attachment; uncertainty/stress	Aggression
McDermott et al. (2009)	MAOA	Provocation	Uncertainty/stress	Aggression
		Parenting		
Gibb et al. (2011)	5-HTTLPR	Expressed emotion criticism	Uncertainty/stress	Attentional bias for angry faces
Gilissen et al. (2008)	5-HTTLPR	Attachment security	Incentive reward; social reward/attachment	Electrodermal reactivity during Trier Social Stress Test for children
Hankin et al. (2011)	5-HTTLPR	Positive parenting	Incentive reward; social reward/attachment	Positive affect
Ivorra et al. (2010)	5-HTTLPR	Maternal anxiety of caregiving	Uncertainty/stress	Irritability of infants

Jacobs et al. (2011)	5-HTTLPR	Maternal depressive history	Incentive reward; social reward/attachment; uncertainty/stress	Adolescent inaccuracy in classifying emotional faces
Kochanska et al. (2011)	5-HTTLPR	Maternal responsive care	Incentive reward; social reward/attachment; uncertainty/stress	Child competence
Luijk et al. (2011)	5-HTTLPR	Parenting sensitivity	Incentive reward; social reward/attachment; uncertainty/stress	Child attachment
Pauli-Pott et al. (2009)	5-HTTLPR	Maternal sensitivity	Incentive reward; social reward/attachment; uncertainty/stress	Negative emotionality in infants
Spangler et al. (2009)	5-HTTLPR	Maternal responsive care	Incentive reward; social reward/attachment; uncertainty/stress	Attachment disorganization
Sulik et al. (2012)	5-HTTLPR	Maternal sensitivity	Incentive reward; social reward/attachment; uncertainty/stress	Child noncompliance
Sonuga-Barke et al. (2009)	DAT1, 5-HTTLPR	Maternal expressed emotion	Incentive reward; social reward/attachment; uncertainty/stress	Conduct disorder
Mills-Koonce et al. (2007)	DRD2	Maternal sensitivity	Incentive reward; social reward/attachment; uncertainty/stress	Affective problems
Propper et al. (2008)	DRD2	Maternal sensitivity	Incentive reward; social reward/attachment; uncertainty/stress	Respiratory sinus arrhythmia
Bakermans Kranenburg & van Ijzendoorn (2006)	DRD4	Maternal sensitivity	Incentive reward; social reward/attachment; uncertainty/stress	Externalizing behavior
Bakermans-Kranenburg et al. (2008)	DRD4	Parenting intervention	Incentive reward; social reward/attachment; uncertainty/stress	Externalizing behavior
Bakermans-Kranenburg et al. (2008)	DRD4	Parenting intervention	Incentive reward; social reward/attachment; uncertainty/stress	Salivary cortisol
Gervai et al. (2007)	DRD4	Disrupted maternal communication	Uncertainty/stress	Disorganized attachment

Knafo (2009)	DRD4	Maternal sensitivity	Incentive reward; social reward/attachment; uncertainty/stress	Prosocial behavior
Propper et al. (2007)	DRD4	Parenting quality	Incentive reward; social reward/attachment; uncertainty/stress	Externalizing behavior
Sheese et al. (2007)	DRD4	Parenting quality	Incentive reward; social reward/attachment; uncertainty/stress	Sensation seeking
van IJzendoorn &Bakermans Kranenburg (2006)	DRD4	Maternal unresolved loss/trauma	Incentive reward; social reward/attachment; uncertainty/stress	Disorganized attachment
van IJzendoorn et al. (2009)	DRD4	Security of attachment	Incentive reward; social reward/attachment; uncertainty/stress	Prosocial behavior: sharing
Jokela et al. (2007)	HTR2A	Maternal nurturance	Incentive reward; social reward/attachment; uncertainty/stress	Depression symptoms
		Positive intervention		
Brody et al. (2009)	5-HTTLPR	Family centered prevention program	Incentive reward; social reward/attachment	Risky adolescent behavior
Cicchetti et al. (2011)	5-HTTLPR	Child–parent psychotherapy and psychoeducational parenting Intervention	Incentive reward; social reward/attachment	Attachment security and disorganization (but only in nonmaltreated children)
Drury et al. (2012)	5-HTTLPR	Foster care versus institutional rearing RCT	Incentive reward; social reward/attachment; uncertainty/stress	Indiscriminate social behavior
Eley et al. (2011)	5-HTTLPR	Therapy	Incentive reward; social reward/attachment	Response to therapy
Bockting et al. (2013)	5HTTLPR	Psychological therapy	Incentive reward; social reward/attachment	Depression
Kohen et al. (2011)	5HTTLPR	Psychosocial treatment	Incentive reward; social reward/attachment	Depression
Andersson et al. (2013)	5HTTLPR, COMT	Cognitive behavior therapy for social anxiety disorder	Uncertainty/stress	Anxiety
van den Hoofdakker et al. (2012)	DAT1	Behavioral parent training	Incentive reward; social reward/attachment	ADHD

Soderqvist et al. (2014)	DRD2	Training in working memory	Incentive reward	IQ, working memory
Beach et al. (2010)	DRD4	Parenting	Incentive reward; social reward/attachment; uncertainty/stress	Alcohol use
Brody et al. (2013)	DRD4	Prevention (alcohol in adolescents)	Incentive reward; uncertainty/stress	Alcohol use
Cleveland et al. (2014)	DRD4	PROSPER Intervention	Incentive reward; social reward/attachment	Alcohol use
Kegel et al. (2011)	DRD4	Early literacy instruction through computer games	Incentive reward	Literacy
Plak et al. (2015)	DRD4	Literacy intervention	Incentive reward	Literacy
Sasaki et al. (2011)	DRD4	Religion priming	Social reward/attachment	Prosocial motivation
Albert et al. (2015)	NR3C1	Fast Track prevention program	Incentive reward; social reward/attachment	Externalizing
		Prenatal stress		
Nijmeijer et al. (2010)	5-HTTLPR	Prenatal and perinatal risk factors (maternal smoking and low birth weight)	Uncertainty/stress	Autism symptoms
Pluess et al. (2011)	5-HTTLPR	Prenatal maternal anxiety	Uncertainty/stress	Negative emotionality
Kahn et al. (2003)	DAT	Prenatal smoking	Uncertainty/stress	Hyperactive–impulsive, inattentive, oppositional behavior
Keltikangas-Järvinen et al. (2007)	DRD2	Birth weight	Uncertainty/stress	Educational achievement
Wiebe et al. (2009)	DRD2	Prenatal smoking	Uncertainty/stress	Irritability, stress, dysregulation, attention, lack of executive control
		Social support		
Fox et al. (2005)	5-HTTLPR	Social support (reported by mother)	Social reward/attachment	Behavioral inhibition
Kaufman et al. (2004)	5-HTTLPR	Social support	Social reward/attachment	Depression in maltreated children
Jokela et al. (2007)	THP1	Social support	Social reward/attachment	Depression symptoms